

BIOLOGY OF *BOMBUS POLARIS* CURTIS AND *B. HYPERBOREUS* SCHÖNHERR
AT LAKE HAZEN, NORTHWEST TERRITORIES
(HYMENOPTERA: BOMBINI)

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Adaptations for survival in a high arctic environment by Bombus polaris and B. hyperboreus are described. For B. polaris, adaptations related to low temperature are: structural characteristics of adults—large size, long dense hair, and dark color; behavioral—nest constructed on surface sites, with entrance facing towards the sun at maximum elevation, and flight by queens and workers close to ground surface. For the short season of growth, adaptations include: development of only a single brood of workers prior to production of sexual forms; eggs of first brood all laid in a single cell, and larvae fed collectively; extended foraging activity by queens and workers in continuous daylight; and acceptance by foragers of a wide variety of flowers. B. hyperboreus is a nest parasite of B. polaris. Adults of B. hyperboreus are similar to those of B. polaris in characteristics not associated with nesting. Shortening of the life cycle of B. hyperboreus was achieved by elimination of the worker caste.

This paper reports studies of various aspects of the biology of *Bombus polaris* Curtis, 1835 and *B. hyperboreus* Schönherr, 1809. The purpose of these studies was to determine how these species have adapted to life in an arctic environment. Investigations were conducted at Lake Hazen (81° 49' N, 71° 18' W), Ellesmere Island, Northwest Territories, Canada, in the study area described by Savile (1964), from May 24 to August 20, 1967 and May 30 to August 28, 1968.

NOMENCLATURE, SYSTEMATICS AND GEOGRAPHICAL DISTRIBUTION

The high degree of polymorphism exhibited by northern species of *Bombus* and lack of communication between North American and European workers in describing new species collected by early arctic explorers has resulted in lengthy synonymies. Not all such problems are yet settled, and an explanation is required to justify use of one of the names in this paper.

Because the name *Bombus arcticus* Kirby, 1824, used by Richards (1931) is a secondary junior homonym of *Apis arctica* Quensel, 1802, which in turn is a junior subjective synonym of *Bombus agrorum* Fabricius, 1793, Kirby's *arcticus* must be replaced by another name. The name *Bombus polaris* Curtis, 1835, a junior subjective synonym of *B. arcticus* Kirby, is available, and is used here as the valid name. O. W. Richards (pers. comm., 1969) accepts this name change.

The species *B. polaris*, *B. hyperboreus* and five others belong to the subgenus *Alpinobombus* (Richards, 1931 and 1968). The group is in need of revision, a task rendered difficult by shortage of material and much variation in physical characteristics among the species. Members of *Alpinobombus* are confined to arctic and alpine tundra in the holarctic-

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region. They are found in the Alps, Arctic Europe, Asia, Greenland, Arctic America, and in the mountains of western North America as far south as Arizona. *Bombus polaris* (Fig. 1) and *B. hyperboreus* (Fig. 2) are arctic and probably circumpolar forms. The apparent gaps in their ranges in Siberia probably represent lack of collecting.

McAlpine (1964, 1965a) indicated that members of only a small number of insect species live in the northwest Queen Elizabeth Islands because of the environmental influences, and that these are extremely tolerant of "harsh" arctic conditions. This harshness of the environment probably excludes members of *Bombus* from some areas. Generally the distributions of *B. polaris* and *B. hyperboreus* are similar; *B. polaris* is recorded from areas where *B. hyperboreus* is absent (i.e. Quebec and Labrador), whereas *B. hyperboreus* is recorded only from areas where some other member (*B. balteatus* or *B. alpinus*) of the subgenus is also recorded. Chernov (1966) and Brinck and Wingstrand (1949, 1951) illustrate this point. The distribution of *B. polaris* and *B. hyperboreus* was determined from the literature and from specimens in the Canadian National Collection and my collection. Records are published by Strand (1905), Sladen (1919), Friese (1923a), Richards (1931), Hellén (1933), Braendegarrd, Henriksen, and Spärck (1935), Skorikov (1937), Henriksen (1937, 1939), Carpenter and Holm (1939), Brinck and Wingstrand (1949, 1951), Yarrow (1955), Savile (1959), Bruggeman (1958), Ander (1965), Chernov (1966), Swales (1966), and Mosquin and Martin (1967).

NESTING

Artificial domiciles

To obtain enough bumblebees to study populations, flight activities, nest temperatures, food preferences, and interspecific associations, attempts were made to attract queens to artificial domiciles placed in their natural habitats. Colonies established in artificial domiciles are easier to study than those in natural nests.

Materials and methods. - I used light weight domiciles of two designs (Fig. 3), each including three parts: a masonite base, a body with entrance hole 19 mm or 25 mm diameter, and a styrofoam top. Tops of one type were inverted blue flower pots, and bodies were pieces of 15 mm shellac-soaked cardboard tubing. Tops of the second type were rectangular white boxes on bodies of ¼ in. plywood. Nesting material of upholsterer's cotton was placed inside each box. Entrance directions varied. Black polyethylene tubing, one foot long, of either 22 mm or 13 mm outside diameter, was connected to the entrance holes of some domiciles to form entrance tunnels. The outer ends were cut obliquely to form landing platforms. Domiciles were placed on the ground with small pebbles, soil, vascular plants and moss over the tunnels. Permafrost barred the use of underground nests. In 1967 200 domiciles in 10 localities and in 1968 180 domiciles in nine localities were used. The domiciles were placed in the field when spring melt commenced. Because many domiciles were damaged by arctic foxes, arctic hares, and musk oxen, fine-mesh chicken wire was secured over the tops of the accepted domiciles to protect them.

Results. - Of the 380 domiciles used in two years, only five were occupied by *B. polaris* queens. Each was of the blue styrofoam flower pot type with a large tunnel. Entrances to three faced between 250° -280° and two faced between 100° -115° range, suggesting no strong directional preference by the bumblebees which occupied them. The domiciles were in four different habitats. At acceptance time, adjacent areas were free of snow, though some melting snow drifts remained on N and NE-facing banks of Skeleton Creek and on slopes in the higher fault zone.

Natural nests

The purpose of this investigation was to discover factors controlling nest initiation by arctic bumblebees. Areas that queens rejected while searching and the habitats in which they eventually established were also investigated.

In the arctic regions, data about nests of various *Alpinobombus* species have been reported by: Jacobson (1898), Friese (1904, 1908, 1923a, and b), Johansen and Nielsen (1910), Frison (1919), Friese and Wagner (1912), Sladen (1919), Brinck and Wingstrand (1951), Freuchen and Salomonsen (1958), Løken (1961), and Milliron and Oliver (1966).

Materials and methods. -Queens in search of nesting sites were observed, and these data were recorded: amount of time spent searching, habitats and sites investigated, possible reasons for rejection of particular sites, temperatures and moisture conditions of the soil, available nesting material, and directions of tunnel entrances. Each queen in natural and artificial domicile nests was marked with nail polish on a particular part of the body as soon as the nest was found so that she could be recognized again.

Date of nest establishment was calculated by subtracting one to six days from the date on which the nest was discovered, depending upon kind and amount of progress at the time (Hobbs, 1964b). Data from the accepted artificial domiciles are included to indicate peaks of establishment.

Areas in which nests occur. -Of 94 natural nests located at Lake Hazen, 92 were on the surface of the ground, one was on a caribou rug in the sleeping tent, and one was in an abandoned lemming burrow. Nests were in marsh and sedge meadows along streams (Skeleton Creek and creek no. 51) and beside pools and tarns (i.e. those in T6, Q7, P6, M10 of Fig. 6). Three nests described by Milliron and Oliver (1966) were also in marsh meadows.

General characteristics and vegetation of marsh and sedge meadows (Fig. 7) and marginal areas around each of the pools and tarns have been described by Savile (1964) and Oliver and Corbet (1966). Plants found¹ in the moister meadows are of *Juncus albescens* (Lge) Fern., *J. castaneus* Sm., *J. biglumis* L., *Eutrema edwardsii* R. Br., *Cardamine pratensis* L., *Saxifraga hirculus* L., and *Ranunculus trichophyllus* Chaix. The principal mosses are *Drepanocladus brevifolius* (Lindb.) Warst and *Bryum* spp. The drier meadow areas are characterized by the dominant *Carex aquatilis* Wahlenb. var *stans* (Drej.) Boot, with varying amounts of *Eriophorum scheutzeri* Hoppe, *E. triste* (Th. Fries.) Hadac and Løve, *J. biglumis*, *Arctagrostis latifolia* (R. Br.) Griseb., *Polygonum viviparum* L., *Salix arctica* Pall. and lesser amounts of *Equisetum arvense* L., *E. variegatum* Schlecht., *Pedicularis arctica* R. Br., *P. hirsuta* L., *Cerastium beeringianum* Cham. and Schlecht., *Saxifraga nivalis* L., *S. rivularis* L., and *Ranunculus sulphureus* Sd. The principal bryophytes are *Drepanocladus revolvens* (Sw.) Warnst., *Orothecium chryseum* (Schultes) BSG., and *Campylium arcticum* (Williams) Broth., and *Bryum* spp. The vegetation forms a closed cover over the partly decaying organic material (Day 1964).

In meadows and marginal pool areas natural nests were on small flat areas, in depressions, and beside small hummocks of moss or other vegetation. Variations in structure were numerous. The majority ($P > 0.005$) of nests (Fig. 5a) examined had entrances which faced in the 180° to 270° quadrant; more (Fig. 5b) faced between 225° and 270° than in the 180°-225° sector. A possible explanation is the sun orientation at the daily temperature peak. The maximum diel soil surface temperature occurred between 1300 and 1600 hours (Corbet 1966, 1967a, b) when the bearing of the sun progresses from 195° to 240°. The highest temperatures around a conical mound of moist moss were at the west, not at the south where the sun's altitude was greatest: surface temperature of the north slope remained almost steady through 24 hours. Also, moss mounds and *Dryas* hummocks in sedge meadows

[¹ Throughout the text, flower nomenclature follows that of Porsild (1964) and Savile (1964) and bryophyte nomenclature is that of Brassard (pers. comm. 1969).]

were the warmest areas and showed exceptionally marked diel periodicities of surface temperatures (Corbet, 1967b). Moderate to light moisture conditions were not deterrent factors in nest establishment for though the nests often became waterlogged beneath they remained comparatively dry on the surface. Nests in the sedge meadows and along the north banks of the streams were drier; the moisture in and around these nests resulted from the later permafrost melt.

In an attempt to discover why surface sites in meadows and marshes were preferred to rodent burrows (the traditional sites of bumblebee nests in temperate areas), temperature data were obtained for both types of sites. Data are presented in Table 1 for abandoned lemming holes at least 30 cm deep which queens had investigated. In a marsh and sedge meadow (M7, Fig. 6) 75 readings were recorded from a grid 25 meters long by eight meters wide (Table 2). Temperatures at the soil surface fluctuate daily, especially during June at Lake Hazen (Powell, 1961; Corbet, 1967b) which may influence the temperature of the marsh and sedge meadows. Soil temperatures measured one foot beneath the surface (Powell, 1961) were lower than temperatures in lemming burrows. The latter were more exposed and more influenced by surface temperatures and solar radiation. Nonetheless, temperatures in the lemming burrows were lower than those in the marsh meadow.

Table 1. Temperatures in abandoned lemming holes when they were investigated by *B. polaris* queens; June 3 to June 23, 1967, and June 15 to July 3, 1968, at Lake Hazen, N. W. T.

	Number of lemming holes investigated	Range	Temperature, °C	
			Mean	SD
1967	26	-1.1 to +3.9	1.20	0.98
1968	39	-1.8 to +2.8	0.64	0.73

Table 2. Soil temperature ranges at 5 cm depth in a marsh and sedge meadow (M7, Fig. 6) at 1400 hrs. on three different days in 1968 at Lake Hazen, N.W.T.

	Air temp 15 cm above ground		Soil Temperature, °C at 5 cm		
		N	Range	Mean	SD
June 17	7.5	75	0.7- 7.0	4.82	1.10
June 25	11.0	75	1.5- 8.5	6.35	1.28
July 2	9.5	75	3.0-12.0	8.28	1.58

Moisture conditions of the burrows examined by queens were also investigated. About 75 per cent of the burrows contained ice or permafrost, or were extremely damp in some part. In contrast, surface moss and liverworts of the marsh meadows were not so affected by ice and permafrost, although they were briefly inundated by the fluctuating water level during snow melt. In summary, surface areas of marsh and sedge meadows were warmer and drier than were most of the lemming burrows.

Emergence of queens and the search for nest sites. - Physiological factors associated with egg development probably stimulate a queen to seek a nest and start a colony (Medler 1962a). The ovaries of *B. (Bombus) lucorum* L. queens in Surrey, England did not develop until after a hibernation period (Cumber 1949) followed by an active feeding period of almost three weeks resulting in a noticeable increase in weight and in a swelling of the ovarioles (Cumber 1949, 1953). At Hazen the pre-feeding period is about a week. After their ovaries mature the *B. polaris* queens search for nesting sites.

The first *B. polaris* queens were observed May 27, 1967 and June 14, 1968, and the first *B. hyperboreus* queens were observed on June 9, 1967 and June 21, 1968. During the first few days of the season, queens visited for nectar and pollen the flowers of *Saxifraga oppositifolia*, the only ones in bloom at the time.

Hunting begins when *Salix arctica* blooms, which is within a week after the first flowers of *Saxifraga oppositifolia* appear. In 1967, searching by *B. polaris* queens extended from June 3 to June 23, and in 1968 from June 15 to July 3. Searching for nests of *B. polaris* by queens of *B. hyperboreus* extended from June 15 to July 16 in 1967, and from June 23 to July 10 in 1968. Searching by *B. polaris* queens reached a peak four to six days after beginning and then declined for the rest of the period. For example, on June 19, 1968, 24 *B. polaris* queens were observed seeking nests, whereas on June 30, only two such queens were observed. The activity of *B. hyperboreus* queens reached a peak seven to 11 days after they became active.

Queens searched in cracks in the soil in clay banked areas, in rocky areas, in marsh and sedge meadows, around *Dryas* hummocks, and in abandoned burrows of lemmings. They even searched the walls and caribou rug floors of the tents. Queens flew throughout the 24 hour period if the weather was favorable, usually less than 25 cm and not more than 30 cm above ground level. They alighted now and then to inspect promising sites more closely.

The lemming burrows investigated were usually those with south to northwest-facing entrances (Fig. 4). Diameters of these tunnels were in the 4-8 cm range. Investigation of a burrow usually occupied less than 30 seconds, but some queens spent up to three minutes in this activity.

Suitable material for construction of bumblebee nests was found in 27 lemming burrows. This material had probably been used in construction of lemming nests and included dried or decaying grasses, sedges, mosses hair, and feathers. Marsh meadows also provided nesting material of mosses, leaves, grasses and sedges. Suitable nesting material was absent from sparsely vegetated areas of saline clay, sand, gravel, *Dryas-Kobresia* habitats, mud and gravel deltas, and most *Dryas* hummock habitats.

Nest establishment for nine *B. polaris* queens observed began on June 7 and ended June 17, 1967. The peak occurred June 9 or June 10 when four of the queens established. In 1968, for eight queens, the period was from June 15 to 25 with no obvious peak. Three queens, while in the process of establishing, abandoned their nests, apparently because of disturbances during examination. Four queens failed to return to their nests after a light snow storm on June 29, 1968 when the screen temperature was 1.0 C.

Nest construction. -Upon accepting a suitable location to establish a natural nest (Fig. 7) or occupy a domicile, a queen completely rearranges the nesting material to form a brood chamber. To loosen and rearrange the moss she pulls it with her mandibles and fore-legs and pushes it under her body to the desired position with her mid- and hind-legs. Queens (and later, assisting workers), continue to rearrange the material so long as the colony is expanding. Most nesting material consists of mosses and liverworts. Names of the principal bryophytes from 92 nests are presented in Table 3. The principal vascular plant-nesting material consisted of dried blades of *Carex aquatilis* and *Eriophorum* spp. with *Equisetum* spp., *Dryas* and *Salix* in some nests. For a complete list of mosses and liverworts from the nests with relative abundance, see Richards (1970). In 1967, representatives of 46 mosses and four liverworts with an average of 7.1 (range 2-14) species were collected from each of the nests; in 1968, representatives of 48 mosses and eight liverworts with an average of 6.7 (range 3-13) species per nest were collected.

Table 3. The principal bryophytes from 92 natural nests of *B. polaris* at Lake Hazen, 1967, 1968.

	Number of nests with moss	
	1967	1968
<i>Barbula icmadophila</i> Schimp ex Mull	10	5
<i>Bryum</i> spp.	38	33
<i>Calliergon giganteum</i> Schimp (Kindb)	11	14
<i>Campylium arcticum</i> (Williams) Broth.	36	25
<i>Cirriphyllum cirrosum</i> (Schultes) Grout	13	1
<i>Distichium capillaceum</i> (Hedw.) BSQ	21	19
<i>Distichium</i> sp.	10	5
<i>Ditrichum flexicoule</i> (Schwacgar.) Hampe	19	19
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	14	8
<i>Drepanocladus revolvens</i> (Sw.) Warnst.	20	28
<i>Orthothecium chryseum</i> (Schultes) BSG	24	29
<i>Tomenthyonum nitens</i> (Hedw.) Loeske	12	10

Nests changed as the season progressed. Earlier the external dimensions were small, about 5 cm diameter, whereas later some were as large as 15 cm. The external covering of the nest cavity was convex-oval with the mosses and dried sedge leaves intermixed to form a thick and tightly constructed surface. The covering of some nests reached a height of 5 cm. Nest cavities were in shallow depressions covered with dried moss, leaves, roots and occasionally peat. The queen and workers excavated parts of the moss mounds beside the nests where the bees defecated.

Discussion.- The factors controlling nest initiation are complex. Whatever physiological factors are involved must take effect either promptly after emergence from hibernation or become effective during the fall feeding period and then again before or during spring emergence. Queens investigate all major habitats for a suitable site. That queens search such areas as lemming holes suggests that in some localities *B. polaris* queens regularly establish underground. This is also suggested by a few publications (Johansen and Nielsen, 1910; Frison, 1919). Another possibility is that underground searching is a trait inherited from the ancestral stock of *B. polaris*.

The habitat in which the queen establishes her nest has the following characteristics; it is warmer than habitats of compact soil, has more suitable nesting material than is present in *Dryas-Kobresia* habitats, or in sand and gravel knoll habitats; it is adjacent to food sources; and it lacks the excessive moisture of the clay, sand, gravel, and *Dryas* hummock areas during nest establishment. I believe that low temperatures of soil or lemming burrows inhibit queens from establishing in such places, even if other factors are favorable. While founding queens are not specific in choosing nesting material, they seem to prefer leaves and bracts of mosses and liverworts.

Interestingly, queens investigated lemming burrows with entrances facing the same direction as sites on which most nests were located. The patterns of distribution and behavior of bumblebees are correlated with the aspect of the slope they inhabit, as is true of many other organisms living in the arctic environment (Corbet, 1967).

COLONY DEVELOPMENT

Colony composition

Among the potential aspects for adaptations of arctic and alpine bumblebees are the physiological and morphological stages of a colony. Because the climatic environmental factors (i.e. low temperature, small heat budget, and reduced growing season) are more severe than in other regions the adaptive developmental changes have become vital in allowing the bumblebees to survive in the high arctic.

There has been little previous work on *Alpinobombus* brood-rearing behavior and all but two of the authors who have investigated the various species, described only the contents of nests at a particular stage when they were collected (Sladen (1919); Frison (1919 and 1927a); Brinck and Wingstrand (1951); Johansen and Nielsen (1910); Milliron and Oliver (1966); Hasselrot (1960); Hobbs (1964a and b); Løken (1961)).

Materials and methods.- Observations and rough sketches were made and photographs were taken of five artificial domicile nests and 24 natural nests at intervals of two to five days throughout the seasons. I determined arrangement and number of eggs, larvae, pupae, and pollen by dissecting the wax-pollen canopy covering the broods. Nests were periodically collected and the brood was examined in the laboratory.

Before I gained experience in removing the protective covering and accidentally touched the brood, the workers removed the eggs or larvae from a recently exposed wax-pollen cell with their mandibles and carried them outside the nest. These larvae were examined and collected. I also observed workers eating the exposed eggs in egg cups an activity which led Brian (1951) to suggest cannibalism. When I exercised care and did not touch the eggs or larvae, the workers repaired the wax-pollen covering over them. During observations, exposure of the nest resulted in temperature drops comparable with those resulting from absence of a queen during foraging (Fig. 17); such additional cooling is not considered to be an important stress factor on brood development. In one instance, a 15 minute observation resulted in a drop in nest temperature of 8.25 C (30.25 to 22 C), in another, a 17 minute observa-

tion resulted in a decline of 10.0 C (31 to 21 C).

First brood.- The following is a summary of observations: After a queen of *B. polaris* completely rearranges the moss or upholsterer's cotton nesting material, she visits flowers of *Saxifraga oppositifolia* or *Salix arctica* and returns to the nest with two pollen pellets. After placing these pellets side by side she builds the wax-pollen first brood cell (Fig. 8) on top of them. The honey pot was built after the brood cell by the nine queens observed. The honey pot is built separately from the brood and in line with the longitudinal axis of the incubation groove. It is sufficiently near the groove that the queen while incubating drinks from it without leaving the brood. Before she builds the honey pot the queen stores honey in the moss and cotton nesting material, providing a small food reserve which also acts as an early insulating layer. Eggs are usually deposited vertically in a single cup, at one time. In one instance the egg cell was probably reopened and additional eggs were laid, for they were in two separate groups within the cell. Egg cells have a definite area under them for fresh moist pollen during larval development. Thus the queen at this stage is a "pocket-maker". The wax-pollen canopy covering the egg cells is a dark brown, rough mass colored by the yellowish pollen of *S. oppositifolia* and *S. arctica*. The incubation groove, although poorly formed on the egg cell, was present in all nests observed.

First brood larvae are fed moist, easily manipulated pollen by the queen. She pushes it under the brood in several places, especially under the sides of the incubation groove. Larvae in front of the incubation groove (toward the nest entrance) were larger and developed more rapidly than those toward the back, because most pollen is pushed under larvae in the former position and the honey pot is nearer to them. After one to three days growth, the larvae lie side by side in a curled position (Fig. 9) allowing easy access to the pollen below. When pollen is plentiful the larvae eat into the mass until they become completely enclosed. Last instar larvae construct separate cells immediately before spinning cocoons and are then fed individually with a mixture of honey and pollen. Often they are such a size that the wax-pollen canopy does not completely cover them. In some nests the color of the wax-pollen covering first the egg cells and then the larvae changes from a dark brown to a lighter tan, owing to a change in the pollen supply.

Cocoons are separated from each other by flimsily spun silk and by the wax-pollen covering. When no fresh pollen is brought into the nest, that already present begins to harden and dry. The incubation groove, evident from the initial egg cell construction, is more pronounced from mid-larval stage to worker emergence.

First brood larvae usually become workers. In one instance, however, three workers and 11 males (imagines and late pupae) were present when a nest was collected. This nest was still developing, for it had an egg cell with 12 eggs and eight two-or-three-day old larvae. The queen had abandoned the nest, apparently because there were fewer workers to assist her in food gathering and incubation, and the few emerged males and workers had depleted the honey. The workers which emerge first are those in the front of the brood nearest the honey pot on the base of the incubation groove. Succeeding emergences progress posteriorly through the incubation groove to the brood furthest from the honey pot. Hence the larger workers emerge first, the small ones later. Marked variation in size of workers within one nest has been reported for other species by Sladen (1912), Cumber (1949), and Medler (1962b, 1965).

Second and third broods (sexuals).- Second and third brood egg cells, also made of wax-pollen material, are built on the outside tops of the cocoons that form the sides of the incubation grooves (Fig. 10). The egg cells are constructed one to two days before or after the first brood larvae begin to spin. Eggs at this time are laid in a horizontal orientation (Figs. 11, 12), with most side by side or on top of each other. In 10 of 13 instances, the

first eggs were placed in the egg cell which occupied the front half of the incubation groove. Usually, one of the ridges of an incubation groove was completely covered with egg cells before any were built on the other ridge. Additional egg cells were not built on the same ridge, until after the first eggs had hatched. As a result, brood in different stages of development can be on the same ridge. No pollen is placed in or under the egg cells to prime the eggs of the second or third broods. The egg cells are small, thick, dark brown wax-pollen cups 6-7 mm long and 3-4 mm wide according to the number of eggs laid in them.

When larvae on the fore part of the incubation groove emerge the wax-pollen canopy covering is not extended to any adjacent or posterior group. Therefore, the larvae beneath the canopy on any ridge are separated and of different sizes on each side of the incubation groove. Fresh moist pollen is pushed into pollen pockets (Fig. 13) beneath the larvae on the edges of the brood when the first eggs hatch. The pollen pots for feeding male and queen larvae are larger than the pollen receptacles under the worker larvae. Bees at this stage of development become "pollen storers." The curled position and pollen diet of second and third brood larvae are identical to those of first brood larvae. Although they built separate cells the last instar larvae were not always completely covered with wax as were the earlier instars. All larvae are fed pollen; larvae of sexuals are also fed honey from the honey pots. Last instar larvae are fed by workers through holes in the wax-pollen canopies.

While the first male cocoons were being spun (Fig. 14), egg cells were still being built; eggs in these cells either did not develop or they were removed by workers. None of the second or third brood in any observed nests were workers. The first egg batches of the sexual brood produced males. Subsequent batches, laid on the remaining part of the incubation groove or on the canopy covering the last instar larvae and early cocoons of the second brood, produced queens (Fig. 15). Males remained in the nest up to two days whereas the queens remained up to seven. The original established queen remained with her nest until after the first males emerged.

Honey pots.- Queens built two or three additional honey pots up to 2-3 cm high and 1-1.5 cm diameter before the workers emerged. These were usually $\frac{1}{2}$ to $\frac{3}{4}$ full. During the season the capacity of each honey pot varied, as first the queen and later the workers added or removed wax. Two small honey pots, one taken from each of two nests while the first brood was in the egg stage, had capacities of 1.12 cc and 1.73 cc. After the workers emerged, as many as 14 honey pots were built (Fig. 16), each usually $\frac{1}{2}$ to $\frac{3}{4}$ full of honey, less full in times of unfavorable weather. Honey was also stored in some of the old worker cocoons and the empty male cocoons, but these storage areas were at most $\frac{1}{4}$ full.

Population structure.- The population of eggs, larvae, and pupae of the first, second, and third broods for each year are indicated in Table 4. Reasons for the variation in egg numbers are unknown. The ratio in spring of females to workers produced was 1:16, and in fall the ratio was 1:3.03 (1967) and 1:1.76 (1968). The numbers of eggs per cell of male and female broods is given in Table 5. Differences in numbers between years and in sex ratio were not statistically significant at the 95% level. The ratio of the number of larvae of sexual forms to the number of workers in 1967 was 1.57; in 1968 it was 1.53. Sex ratios within each nest were in 1967, 2.0 males per female and in 1968, 1.6 males per female. Although queens were successful in rearing almost all first brood workers to maturity, they were less successful with second and third broods. Of those nests studied during the entire seasons of 1967 and 1968, mortality before emergence of adult males was 57.1% and 37.2% and of adult females was 62.5% and 41.0%.

Table 4. Numbers of first, second, and third broods of eggs, larvae, and pupae from nests of *B. polaris* at Lake Hazen, N.W.T., for 1967 and 1968.

	First brood (worker)		Second brood (male)		Third brood (queen)	
	N	Range	N	Range	N	Range
1967						
Egg	2	16-17	8	4-34	8	8-23
Larvae	6	14-17	7	4-23	8	2-18
Pupae	8	13-17	5	2-15	5	2- 6
1968						
Egg	2	15-17	6	6-24	6	11-18
Larvae	7	15-17	8	8-24	7	3-16
Pupae	6	14-19	7	4-24	5	5-16

Table 5. The numbers of eggs per egg cell of *B. polaris* male and female broods per year in the artificial domicile nests and natural nests at Lake Hazen, N.W.T.

	Male		Female	
	N	Range	N	Range
1967	21	2-13	18	4-17
1968	11	3-14	10	5-12

Times required for development of each stage and each brood of *B. polaris* for each year, are given in Table 6.

Discussion.- Species of *Alpinobombus* differ from one another and from members of other subgenera in oviposition characteristics, colony size, brood composition, and length of time required to complete stages of the life cycle. As an illustration of subgeneric differences, data for *B. balteatus* (Hobbs, 1964a, b) are aligned with my data for *B. polaris* (Table 7).

Table 6. Duration of development in days of eggs, larvae, and pupae of first, second, and third broods of *B. polaris* at Lake Hazen, N.W.T., 1967 and 1968

	First brood (worker)		Second brood (male)		Third brood (queen)	
	N	Range	N	Range	N	Range
1967						
Egg	5	3.5-4	7	3.5-4	7	3.5-4
Larvae	9	7.0-9	3	9.0-11	4	7.0-9
Pupae	8	7.0-9	3	7.0-11	4	9.0-11
Total (egg-adult)		17.5-22		19.5-26		19.5-24
1968						
Egg	1	3.5-4	3	3.5-4	2	3.5-4
Larvae	3	7.0-8	3	7.0-9	2	6.0-8
Pupae	4	6.0-11	4	9.0-14	5	9.0-13
Total (egg-adult)		16.5-23		19.5-27		18.5-25

Table 7. Differences between the composition and development of brood of *B. polaris* and *B. balteatus* (data for *B. balteatus* after Hobbs 1964b).*B. polaris**B. balteatus*

First brood

- all eggs deposited at one time
- average no. of eggs in four broods 16.24
(range 15 - 17)
- average no. of larvae in 13 broods 15.9
(range 14 - 19)

- not all eggs deposited at one time
- average no. of eggs in eight broods 11
(range 7 - 21)
- average no. of larvae in five broods 14
(range 12 - 15)

Sexual brood

- eggs laid on same ridge of incubation groove were of different ages and castes
- wax-pollen canopy covering larvae of adjacent cells not extended to cover all larvae on the same ridge
- only one brood of workers produced before males and queens

- eggs laid on same ridge of incubation groove were of different ages but same caste
- wax-pollen canopy covering larvae of adjacent cells extended to cover all larvae on the same ridge
- sometimes more than one brood of workers produced before males and queens

Queens of *Alpinobombus* colonies are the only bumblebees known to place all eggs of the first broods in single egg cells. The numbers of eggs laid per cell for second and third broods of *B. polaris* (and probably for other species of *Alpinobombus*) were the same as those laid in succeeding worker and sexual cells by queens of the subgenera *Bombus* and *Cullumano-bombus*, and were greater than the numbers laid by queens of *Subterraneobombus*, *Fervidobombus*, *Pyrobombus* and *Bombias*. The last-named is the only subgenus known of which queens lay only a single egg per cell for the second and succeeding broods (Hobbs, 1964a, 1965a).

More eggs per brood are laid by queens of *B. polaris* in the first three broods than are laid by queens of most other species of bumblebees. However, because of environmental factors restricting total number of broods, seasonal egg production overall is less for arctic species than for those inhabiting warmer areas, farther south.

Colonies of *Alpinobombus* species produced more workers in the first broods than did colonies representing most other sub-genera studied by Hobbs (1964-1968). It is difficult to estimate values for workers per queen in fall for species with colonies living under warmer conditions in lower latitudes because of the wide variation in numbers of workers among different colonies. Generally, however, values for this ratio are about the same for both temperate and arctic-alpine species.

Colonies of *Alpinobombus* species are small because usually only a single brood of workers is produced before a queen begins to produce the sexual broods (Hobbs, 1964a). Queens of other subgenera produce at least two worker broods—hence more workers— than *Alpinobombus* colonies produce. Among other subgenera, limited data suggest that number of workers per colony varies with latitude: the Holarctic arctic-alpine *B. (Pyrobombus) sylvicola* Kirby has as many as 139 worker cocoons (Hobbs, 1967b), whereas the tropical *B. medius* produces as many as 2183 workers (Michener and La Berge, 1954).

The paucity of workers led Friese (1902, 1908, 1923a and b) and Friese and Wagner (1912) to suggest that arctic bumblebees including *Alpinobombus* species are tending toward a solitary mode of life. I do not believe that this is so. Rather, I think that the reduced colony size is adaptive to life under arctic conditions. Certainly, queens of these northern taxa behave toward their broods as social insects, just as do their southern counterparts.

Hasselrot (1960) reported that rates of development of the various life stages and larval instars of a selection of *Bombus* species were similar to one another. Mean values for all species studied were as follows: egg stage - 3.4 days; larval stage - 10.8 days; pupal stage - 11.3 days; total average time of development - 24.5 days. The rate of development is comparable to the above data for the life stages of *B. polaris* (cf. Table 6).

Brood reduction in the form of mortality of immatures of *B. polaris* at Lake Hazen was the result of cannibalism and lack of food. The latter is related to periods of unfavorable weather (about 4.0 C to 2.0 C, wind 8-12 mph, and complete cloud cover) during which workers had difficulty in foraging and the food supply within the colonies became depleted (i.e. honey pots less than 1/3 full and scarcity of fresh moist pollen). Under these conditions, workers demolished egg cups and eggs and removed larvae from the nest, thus probably killing them. Food sources were also influenced by unfavorable weather as nectar secretion was reduced and stamens became devoid of pollen.

Mortality data for the observed colonies of *B. polaris* are insufficient for detailed analysis because not all second and third brood egg cells were opened to determine the maximum number of eggs laid. However, the data available suggest that colonies in artificial domiciles had fewer deaths than had colonies in natural nests, possibly because of the insulating effect of the styrofoam tops. Cumber (1949) estimates at least 50% mortality before emergence of

adults for bumblebees in general, and Brian (1951) estimates mortality of *B. agrorum* Fabricius colonies based on all broods except the last, for two years, at 64 and 69 per cent.

At Lake Hazen, bumblebees are one of the few groups of insects to use most of the period of active growth. Adults are active soon after the first flowers bloom in June, continuing until early in August when few flowers are left. Progression of brood development parallels progression of weather and plants.

Flight activity

This is a sensitive indicator of foraging conditions in the field, and of the ability of colonies to exploit available food sources. Rate of food acquisition strongly influences reproductive capacity, and tempo of most activities within colonies of honey bees (Gary 1967), and the same principles may be applied to bumblebee flight activity. The purpose of this study was to characterize weather conditions affecting the foraging of arctic bumblebees, adaptations of the bees to the weather conditions, frequency of flight per 24 hours, and type of food (pollen or nectar) exploited.

The effect of weather and general climatic conditions on bumblebee flight is important, especially in arctic areas, where continuous daylight during the summer permits maximum frequency and duration of this activity (Jacobson 1898 in Friese 1904, 1908, 1923a, b, and Friese and Wagner 1912; and Johansen and Nielsen 1910; Sladen 1919; Frison 1919; Løken 1949, 1954; Longstaff 1932; Bruggeman 1958; Freuchen and Salomonsen 1958; Savile 1959; Hasselrot 1960; Gavriiliok 1961; Downes 1964; Hocking and Sharplin 1964; and Milliron and Oliver 1966). Structural features of possible adaptive significance, such as large size, hairiness, and melanism, and some physiological factors affecting foraging in cooler weather are discussed.

Materials and methods.- In 1968, 24 hour observations were made every six days for 36 days at an artificial domicile. These six series of observations were made at the following six stages of development: (1) first brood mid-larval; (2) first brood early-pupal and second brood egg; (3) first brood emergence, second brood late-larval to early pupal, third brood egg; (4) second brood late-pupal, third brood mid-larval; (5) second brood early emergence, third brood pupal; and (6) third brood late-pupal to early emergence. Six supporting series of observations from a natural nest at unspecified intervals of hour and day, and occasional flight activity observations at an artificial domicile in 1967 were also made. The brood composition and population of the nests were recorded the day before each observation. Thus, the flight activity of bumblebees at major brood development periods was characterized.

Flight was observed from a seated position far enough from a nest to avoid disturbing the bees but near enough to recognize the caste (queen or worker) and presence or absence of pollen on legs. When reference is made to 'pollen load' or 'pollen-gathering' it is assumed that a bumblebee was often also carrying nectar (Brian 1952; Free 1955b). The terms 'nectar load' and 'nectar-gathering' are used only when the forager in question has not been gathering pollen (Free 1955b). For each flight the times (Eastern Standard) of departure and return, the caste of the bee and whether it carried pollen, were recorded. Air temperature was taken initially with a thermistor probe and later with a dial thermometer. Wind velocity in mph and wind direction were estimated with a portable floating ball-type anemometer. All were taken near the nest at a height above ground of 20-30 cm. Cloud cover was estimated visually. Several readings of air temperature, wind velocity and direction, and several estimates of cloud cover throughout each hour of observation were averaged to increase reliability of the data. Solar altitude was taken from Corbet (1966).

For each bee observed away from the nest entrance the following notes were taken: species, caste or sex, time, air temperature, flying height above ground, wind direction and ve-

locity at this height, and cloud cover.

Frequency of food collecting at the nest entrance.- The integral components affecting flight activity were the responses of foraging bees to intra-nest stimuli and to meteorological conditions. Various combinations of light, temperature, wind, and humidity affected bumblebee flight, and might be sufficient to bring about periodicities in flight. Thus, diel periodicities of weather factors near the ground at Lake Hazen (Corbet 1966, 1967b) are considered (Table 8). Jackson (1959a, b) reported for Lake Hazen that for 76% of the observations the average wind velocity from June 1 to August 2 was 5 mph or less. The predominant wind direction was NE, along the Lake Hazen trough (Jackson 1959b, 1960; Corbet 1966, 1967b) followed by ENE, E, and NNE (Corbet 1966). Cloud cover did not exhibit diel periodicity, but a tendency was noted for opacity to increase slightly between 1300 and 2200 hours (Corbet 1966)

Many of the diel fluctuations were obscured by weather trends persisting longer than a day, such as barometric pressure, wind velocity, and cloud cover. The most regular are those resulting directly from solar radiation at or near the soil surface (Corbet 1966).

Table 8. Diel ranges of times of maxima and minima of weather factors near the ground at Lake Hazen, N.W.T. (after Corbet 1966).

Weather factor	Maximum	Minimum
Solar altitude and short wave radiation	1000-1600	2200-0200
Soil-surface temperature	1300-1600	0100-0300
Stevenson screen temperature	1300-1900	0100-0700
Relative humidity	0100-0700	1300-1900
Wind velocity (at 41 feet)	1900-2200	1600-1900

The frequency of flight and the number of pollen and nectar loads collected on various days by foragers of *B. polaris* from an artificial domicile are shown in Figs. 17-22 and those for a natural nest are shown in Figs. 23-26.

Before workers emerged, the queen (Fig. 17) flew at all hours with approximately equal frequency, collecting more pollen than nectar to feed the first brood larvae. The queen was absent from the nest approximately 30 minutes on each of 20 foraging trips. After each forage she deposited pollen and nectar into pollen pocket(s) and/or honey pot(s) and warmed the brood to a temperature comparable to that of the nest before her forage. When the first brood was in the early pupal stage (Fig. 18) the queen collected pollen, but the frequency of her flights was less than during larval development.

The climax of worker foraging activity occurred between July 6 and July 16 when nutritional requirements of second and third brood larvae were maximal (Fig. 19 and Fig. 20). These larvae were fed mixtures of pollen and nectar. The proportions of pollen loads to nectar loads collected by foragers for these two days were 2.20:1 and 1.14:1 respectively. Thus, there is perhaps a difference in the proportions of pollen to nectar fed to the second and third brood larvae. Throughout July 6 the amount of pollen foraged remained nearly the same, whereas nectar gathering reached a peak during 1200 to 1600 hours. On July 12,

however, the pollen gathering peak was between 1000 and 1400 hours and nectar-gathering was proportionately higher most other times. Collectively nectar- and pollen-gathering occurred between 1200 and 1600 hours on July 6 and between 0900 and 1500 hours on July 12. The highest number of worker bumblebees (37) passing through the nest entrance in one hour was counted at about 1400 hours on July 6. On July 12 workers flew until 2330 and no foragers spent the night away from the nest.

The queen and workers foraged primarily for nectar when adults of the second brood began to emerge and during the third brood pupal period (Fig. 21). This corresponds to increase in number of honey pots, to feeding of second and third brood larvae quantities of honey, and to feeding of newly emerged adult males. Males ate honey immediately after emergence. The queen flew 24 hours a day, but at infrequent intervals. She remained away from the nest for longer periods than during the period of sexual larval development and departed permanently soon after the first males emerged.

Peak flight activity for workers was between 1000 and 1700 hours and was not, as yet, a complete 24 hour activity. Flight activity was restricted by food shortage in keeping with reduced nutritional requirements. The population of the nest was also reduced because some foraging workers had died.

On July 24 (Fig. 22), newly emerged third brood queens and some workers were observed in flight at the nest entrance. All collected only nectar. The new queens and workers flew throughout the 24 hour period with no definite peak in activity. The nutritional requirements of the nest were low as the development of the colony was completed, but nectar-gathering was necessary for maintenance of the sexual and worker forms and for preservation of a sufficiently high nest temperature for emergence of the remaining fall queens. Once males had left the nest they did not return.

Weather conditions affected the queen little while she provided for the nest (Fig. 17-18), however she remained within the nest, presumably incubating, during light snow storms on June 17, 1967, and on June 29, 1968. Air temperature at 30 cm above the nest on June 17 was -0.5 C and on June 29 was 4.5 C. Internal nest temperature on June 29 in an artificial nest was 27.0 C and in a natural nest was 19.5 C.

Generally, cloud cover, wind direction, and wind velocity had little influence on frequency of worker flight from the nest entrance. On July 12, 1967, however, mean wind velocity from 0815 to 2230 hours at 15 cm above the ground was 12 mph from the SE (range 7-18 mph), causing approaching workers to land or to be blown to the ground. There, they walked or remained behind the protection of *Salix* and *Saxifraga* clumps before continuing to the nest entrance. Foragers flew into the wind while leaving and returning to the nest when the wind velocity was above 8 mph and did not fly orientation circles. Light showers on July 24 (Fig. 22) reduced flight activity slightly.

The climatic factors affecting circadian periodicity are temperature and sky illumination (Marler and Hamilton 1967), the latter depending mainly on the altitude of the sun. During the part of the season when the workers were flying, the maximum solar altitude varied by three degrees, but within a day the difference between maximum (solar noon) and minimum (solar mid-night) altitude was about 16 degrees. Bumblebee workers did not begin to forage in the morning until the sun was at least 18 degrees above the theoretical horizon. Yet they continued to forage when the altitude of the sun was below 18 degrees for longer periods each day until by July 24 they were flying 24 hours. Thus toward the end of the season the 24 hours of illumination modified any existing periodicity.

Starting about 9-10 C increases in the diel fluctuations of air temperature were correlated to increase in the frequency of flight, and maximum diel air temperature corresponded closely to peak flight activity.

Throughout a season the tendency for food acquisition to shift from pollen-gathering to nectar-gathering and the tendency of foraging hours each day to increase to 24 are behavioral responses to the prevailing weather conditions, to food availability, and to the nutritional requirements of the brood.

The flight activity at the natural nest (Figs. 23-26) was similar to the flight activity at the artificial domicile and any variations (i.e. foraging and brood populations, nutritional requirements) were in the respective nest developments. However, the natural nest queen foraged longer than the artificial domicile queen.

On July 12, 1967, at an artificial nest, the peak of activity was from 1400 to 1800 hours with 57 of 95 workers observed bringing pollen to the nest. The queen and workers did not fly throughout a 24 hour period on that day. Subsequent flight activity observations had ceased by 2200 hours, and by July 19 the flight activity had ceased before 0100 hours.

Flight in the foraging area.- Data about duration of flight activity of *B. polaris* workers, males and fall queens, and of *B. hyperboreus* males and fall queens are presented in Table 9. The flight of *B. polaris* workers began in 1967 and 1968, 32 and 18 days respectively after the first *B. polaris* queens had been observed flying and only one day after the first workers had emerged from the brood cocoons. Although flying conditions were favourable until mid-August, no workers were observed to forage after the given dates.

Table 9. Seasonal duration of flight activity of castes and sexes of *B. polaris* and *B. hyperboreus* at Lake Hazen, N.W.T., 1967 and 1968.

Caste or sex	1967	1968
<i>B. polaris</i>		
worker	June 27 - August 10	June 2 - August 5
fall queens	July 21 - August 7	July 23 - August 3
males	July 16 - August 10	July 21 - August 5
<i>B. hyperboreus</i>		
fall queens	July 24 - August 6	July 24 - August 4
males	July 19 - August 6	July 23 - August 6

Generally the flights of bees distant from the entrance was more difficult to record, because on any one day as few as two or three or as many as 66 bees were observed. Thus, the nest entrance flight activity was a more sensitive indicator of field foraging conditions.

Bumblebees flew in close proximity to those habitats where natural nests were located, that is, the distance from the nest that foragers flew was limited.

As low temperatures tend to restrict flight and wind disrupts the warm air produced by insolation of the soil surface (Downes 1955), height of flying above the soil and corresponding air temperature are considered important. The profile of air temperature above the soil surface was measured at a sandy-clay soil site by a thermistor air probe at 1400 hours four times during the summer of 1968 at varying heights. These profiles (Fig. 27) resembled those recorded at Lake Hazen by Powell (1961) and Corbet (1967b) on different days of the season. Abrupt increases occurred within 5 cm of the ground. The pattern was the same for cloudy and windy days (July 15, July 31) and nearly clear calm days (June 30, July 5). On these four days the air temperature was about 7.75 to 10.25 C at the estimated maximum height of flight of queens and workers, and temperature near ground level was about 10.0 C.

Bertram (1935) studied experimentally effects of minimum temperature on *B. polaris* individuals and found that at 9.5 C the bees no longer retained their normal effective activity and at 5 C they became inactive. However, I have observed four queens foraging for nectar from *S. oppositifolia* at - 1.7 C. Gavrioliok (1961) reported that bumblebees did not work in temperatures below 4.5 C, nor in frosty fog. At Lake Hazen, bumblebees flew most often at temperatures between 7 and 10 C, although early in the 1967 season, queens flew at temperatures between - 1.7 and 4.4 C.

Discussion.- Nutritional requirements and other stimuli originating within the nest affect flight activity. Measurements of honey bee flight at the nest entrance permit a rapid evaluation of the relative effects of intra-nest stimuli (Gary 1967), and this should apply as well to bumblebee colonies. Responses of foraging bees to various combinations of meteorological conditions are as numerous and complex as those to the intra-nest stimuli. One factor predominates at these high latitudes; the daily range of light intensity in clear weather is small, and insects are unable to use the 24 hour light rhythm to synchronize an endogenous cycle (Corbet in Downes 1965). Nonetheless, shifts in flight activity occurred. The queens ceased flying throughout 24 hours when the workers commenced foraging, only to resume again near the end of the season. The workers gradually increased the daily duration of foraging until at the season's end they were flying throughout the 24 hours. But when the colony required the maximum amount of food during development of second and third brood larvae, the queen and workers did not fly throughout the 24 hour period from the nests I observed. However, I believe the workers, shortly after emergence, take their cue for a 24 hour rhythm from the height and position of the sun. Hocking and Sharplin (1964) state that the activity curve for honey bees transported to Lake Hazen was synchronized with Hazen solar time and was unlikely to be due to temperature, since at this latitude the difference between mean maximum and mean minimum temperature during the summer months is less than 5 C. The gradual daily increase in duration of flight activity in response to the 24 hours of light is a significant response to meteorological conditions and may be an adaptation to arctic conditions. Although not statistically tested, other meteorological conditions, such as low air temperature, wind direction and wind velocity, cloud cover, and humidity had less influence on the frequency of flight.

My results indicate that the type of food collected (pollen or nectar) was determined mainly by the brood's nutritional requirements. These depended on the nature and amount of food stores in a colony and especially on the presence and age of larvae in the brood. Collection of food by arctic bumblebees follows the characteristics of lower latitude bees. Number of pollen loads and nectar loads collected at various times of the day by foragers, and the proportion of pollen to nectar loads, shifted gradually from nearly complete pollen-gathering during larval development to nectar-gathering during pupal development. Free (1955a, b) found that the proportion of pollen loads to nectar loads increased during the

day and that the foragers collected pollen only when the carbohydrate stores of their colony had reached a certain minimum level. However, Hasselrot (1960) reports no clear tendency to a forenoon or afternoon preference in pollen-gathering on separate days. Variation of the proportions may indicate the stage of colony development.

Bumblebees develop considerable heat from the activity of the flight muscles (Newport 1837, Hasselrot 1960) and the long shaggy hair of members of *Alpinobombus* enables them to keep active in low temperatures (Sladen 1919, Friese 1923a). During flight, size of the insect and density of the coat are more important for insulation than length of the hair, though they seem to be of negligible value when at rest (Church 1960).

Arctic bumblebees show pronounced melanism and members of the species *B. (Alpinobombus) balteatus*, *B. (Pyrobombus) melanopygus* Nyl., *B. (P.) mixtus* Cress., *B. (P.) sitkensis* Nyl., *B. (P.) sylvicola* Kby. of the Boreal Cordilleran transition zone of Alberta (Hobbs 1967b) also have a tendency to melanism. This dark coloration, generally rare in the North American bumblebee fauna (Sladen 1919), increases absorption of solar radiation. The ability to be warmed by solar radiation is greater in workers because of their reduced size and resulting greater ratio of area to volume (Downes 1926). Thus, large size, long, dense hair and dark coloration are factors which allow bumblebees to be warmed by solar radiation. The relatively low height of flight suggests that bees obtain warmth from radiation reflected from the soil.

Nest temperature

Bumblebees, like some other social Hymenoptera, are capable of partly regulating their body temperatures independently of external air temperatures, and can, singly or collectively, regulate nest temperature. A study of temperature relations of arctic bumblebee colonies at various stages of development was made to estimate brood temperature. Effect of arctic climatic conditions on brood temperature is discussed and a comparison is made between temperatures of the artificial domicile and a natural nest.

Data on the meteorological conditions and diel periodicities affecting brood temperatures were presented in the flight activity section. Previous investigations of temperatures in bumblebee nests were by Himmer (1933), Nielsen (1938), Hasselrot (1960), Wójtowski (1963a, b), Newport (1837), Plath (1934), Cumbér (1949), and Brian (1952). Fye and Medler (1954) gathered temperature data from bumblebee nests in domiciles of varying construction and insulation. Hobbs, Nummi and Virostek (1962) investigated behavioral mechanisms of temperature control in above-ground artificial domiciles. Newport (1837), Sladen (1912), Free and Butler (1959), and Hasselrot (1960) reported heat generation and temperature regulation by the body temperature in nests.

Material and methods.- Measurements of brood temperature and flight activity investigations at the nest entrance were made at the same time. Prior to July 6, temperatures were taken with surface thermistor probes placed under, and (Fig. 10) as near as possible to, the center of the first brood larvae. After July 6, brood temperatures within each nest were recorded each hour with a dial thermometer. Temperatures of the brood were measured at one to two minute intervals while the queen was foraging, to determine fluctuations and dependence of the first brood on the queen for incubation temperature.

Results.- Temperature curves obtained for the artificial domicile nest (Figs. 17-22) and for the natural nest (Figs. 23-26), reflect the development of the colonies.

While only the queen was incubating the brood (Figs. 17-18), variations in nest temperature were related to her absences and were numerous during first brood larval development (Fig. 17). On 20 occasions (Fig. 17) and at different air temperatures, the nest temperature decreased an average of 0.22 C per minute while she foraged. The average rate of increase on her return was 0.43 C per minute, and on the average 14.5 minutes elapsed before the original temperature was attained. Thus the temperature of the brood increased about twice as fast as it decreased while the queen was away, presumably because of brood metabolism. On seven occasions while the queen foraged during first brood pupal development nest temperature decreased at an average rate of 0.30 C per minute and increased 0.27 C per minute on the average when she returned. On average, 22 minutes elapsed before the former nest temperature was attained. The different rates probably result from the lower resting metabolism of pupae.

Queens remained in the nest a longer time after greater temperature drops (e.g. Fig 17, from 1225 to 1545 and Fig. 18, from 1320 to 1625). When these lengthy compensations occurred the nest temperature was as low as or lower than 21 C which may be the minimum temperature for normal first brood larval and pupal development. During this stage maximum nest temperatures are related to the higher air temperatures, but not to the maximum diel temperature, which occurred between 1300 and 1600 hours (Corbet 1966, 1967b). The differences between nest temperature and air temperature were 19 to 22 C. The minimum nest temperatures while the queen was in the nest are related to the minimum air temperatures with differences of 20 to 24 C. Hasselrot (1960) termed this period of instability and variation the "period of upbuilding." During the "period of equilibrium" (Hasselrot, 1960), the nest temperature was 18 to 24 C higher than the outside temperature. The variations for July 6 (Fig. 19), were between 30 and 35 C, and for July 12 (Fig. 20) were between 27 and 33 C. The tendency for the nest temperature to vary in accordance with the variations in the external temperature was not noted in the artificial domicile at this stage of brood development.

During the "period of decline" (Hasselrot 1960), (Figs. 21, 22) temperatures gradually decreased and variations for July 18 (Fig. 21), were between 19 and 28 C with the maximum nest temperature 5 to 7 C warmer than the maximum air temperature and the minimum nest temperature 13 C warmer than the minimum air temperature. Nest temperature variations for July 24 (Fig. 22), were between 10 and 20 C with 5 to 8 C difference from the air temperature.

External air temperature fluctuations influenced the natural nest temperature (Figs. 23-26) more than the temperature of the artificial domicile nest. In addition to those climatic conditions resulting directly from solar radiation, other climatic factors, such as light snow and rain, had more influence on the natural nest than on the artificial domicile nest. Data indicating the insulating effects of the styrofoam are shown in Fig. 18.

Discussion.- The three periods of nest temperature sequence (Hasselrot 1960) were clearly discernible in the artificial domicile nest. The period of upbuilding was characterized by temperature variations caused by absence of the foraging queen. Because the volume of the nest had increased during development of first brood pupae and second brood eggs, the rate of rewarming was slower and time required by the queen to rewarm the nest was longer than during first brood larval development. The period of equilibrium was characterized by stable nest temperatures not in accordance with the outside temperatures. As this was the period of maximum nest population, maximum flight activity, and maximum nutritional requirements, maximum continuous nest temperature was expected. These higher temperatures provided optimum conditions for the work and growth of the colony, and are desirable factors for queen production (Cumber 1949). The period of decline was characterized

by gradually increasing variations in nest temperature which closely agreed with the outside temperature. Decline in the nest temperature is probably connected to the lack of honey in the colonies, caused by the sexual forms using up the supply, and by the disintegration of the colony (Hasselrot 1960).

Results of 24-hour temperature readings in the artificial domicile nest indicated that maximum and minimum nest temperatures were close to the maximum and minimum diel air temperatures. Worker foraging movement in or out of the nest appeared not to influence the nest temperature. Because of the few lengthy observations, the temperature phenology in the natural nest could not be followed, but I believe that it would be the same as for the artificial nest.

The natural nest temperature was more dependent on the external air temperature and the brood was subjected to more severe environmental factors than the artificial domicile nest which had the protection of the styrofoam lid. Even with these nest temperature differences, the time did not vary for each brood to complete development. Generally, more eggs, larvae, pupae, emerging adults of the second and third broods, and food were found in the artificial domicile nests than in the natural nests.

The danger of overheating the nest through excessive insulation is, according to Himmer (1933), very small. Workers of *B. polaris* increased the air flow and regulated temperature of the domicile nest by fanning with their wings at the tunnel entrances. Hasselrot (1960) found that workers began to vibrate their wings at a nest temperature of about 33 C and 13 C in the surrounding air. Workers were not observed to fan any of the natural nests; small ventilation holes in the wax-pollen and moss canopies were present.

Nest temperature curves obtained for these arctic bumblebees were similar to the temperature curves obtained by Himmer (1933), Nielsen (1938), Hasselrot (1960), and Wójtowski (1963a, b) for members of other species of bumblebees.

Food preference

Competition among insects for available nectar and competition among plants for services of pollinating insects have been discussed by several authors (Knuth 1906-1909; Clements and Long 1923; Grant 1950; Brian 1954; Hocking 1968). The purposes of this section are to establish adaptations and relationships of arctic bumblebees to arctic flowers. The phenology and constancy of visitation and usage within the nest were investigated.

The literature on flower constancy for all Apidae was reviewed by Grant (1950) and Brian (1954). Høeg (1924, 1929) reported on degree of constancy to pollen of various species exhibited by bumblebees from Novaya Zemlya and Ellesmere Island. Cockerell and M'Nary (1902) suggest that arctic bumblebees visit a great variety of plants because they have few competitors, but McAlpine (1965b) and Hocking (1968) disagree. In the arctic regions, pollination biology of plants, and pollen on bumblebees have been investigated by McLachlan (1879), Ekstam (1894, 1897, 1899), Jacobson (1898), in Friese (1902, 1904, 1908, 1923a,b), Sparre-Schneider (1906), Johansen and Nielsen (1910), Frison (1919), Sladen (1919), Johansen (1921), Høeg (1924, 1929), Richards (1931), Longstaff (1932), Brinck and Wingstrand (1951), Holmen (1957), Bruggeman (1958), Freuchen and Salomonson (1958), Savile (1959), Gavriliok (1961), Løken (1961), Swales (1966), Milliron and Oliver (1966), Mosquin and Martin (1967) and Hocking (1968).

Angiosperm pollen is the main source of protein (Auclair and Jamieson 1948, Weaver and Kuiken 1951), fat (Hügel 1962), vitamins (Schwarz and Kock 1954, Bukatsch and Wildner 1956) and minerals (Lubliner-Mianowska 1956) which a bumblebee colony needs to maintain itself.

Sugars (carbohydrates) present in the nectar of flowers of various species have been investigated by Wykes (1952a). She found that mono- and oligosaccharides (fructose, sucrose, and glucose) were in nectar of nearly every species tested. Traces of maltose, melibiose, and raffinose were in nectar from flowers of some species. Studies by Park (1930), Hocking (1953, 1968), Wykes (1950, 1951, 1952a, b, c), Manning (1956), and Shuel (1967) show that volume and total sugar concentration of nectar secreted by individual flowers varied widely, both intra- and inter-specifically. Thawley (1969) reviewed the composition and properties of honey.

Sladen (1912), Plath (1934), Free and Butler (1959), and Knee and Medler (1965) described two types of honey found in bumblebee nests: "thin" and "thick." Sladen (1912) described thin honey as that found in wax honey pots constructed by the established queen and later by workers. He believed thin honey was freshly gathered and consumed each day. Thick honey was recorded from old empty cocoons and was considered to be stored for times of scarcity.

The annual duration of growth and seasonal succession of flowering of plant species (Sørensen 1954, Hocking 1968), is significant to the survival of bumblebees especially during August and September when flowers become scarce. Sørensen (1941) in northeastern Greenland distinguished five phenological seasons, which followed each other in rapid succession and which Powell recognized as being shorter in duration at Lake Hazen. Powell (1961) compared the phenology of Lake Hazen, with Alert, Northwest Territories, and Eskimonae, Greenland. Hocking (1968) indicated seasonal peaks for four common species of plants during three years.

Materials and methods.-Observations of bumblebee foragers on flowers at Lake Hazen include records of flower species, constancy, and possible flower pollinating mechanisms.

To support visual observations and to indicate which flowers were used and why, 406 samples of pollen and nectar were taken from 15 nests in 1967 and 134 samples from 22 nests in 1968. Samples were taken throughout the summer during each brood observation. The samples consisted of fresh moist pollen from under the larvae and pupae, from the corbiculae of incoming or field foragers, from wax from honey pots, from brood and canopy, from nectar from the honey pots and brood, and from fresh bee feces.

Pollen and nectar from the nest and pollen from corbicular loads were mounted in glycerine jelly tinted with basic fuchsin for identification by comparison with photographs of samples in a reference collection of flowers in the research area. Pollen identifications were based on sculpture and form only.

Flower preferences.- The phenology for 1958 from Powell (1961) and for 1962 from Savile (1964) and from my two summers' work is presented in Appendix II, of Richards (1970). A comparison of dates for these four seasons at Lake Hazen shows tremendous variation but indicates the sequence in which "bumblebee flowers" are visited and used.

Data about phenology of bumblebee flowers, date of first occurrence of *B. polaris* queens, workers, and males and the period of utilization for 1967 and 1968 are presented in Fig. 28, which was constructed from nest samples of pollen and nectar and from dates of observations. Table 10 summarizes data from observations of the flower species which individuals of *B. polaris* and *B. hyperboreus* visited.

Table 10. Number of observations of *B. polaris* and *B. hyperboreus* individuals at flowers of various species at Lake Hazen, N.W.T., 1967 and 1968.

	<i>Bombus polaris</i>				<i>Bombus hyperboreus</i>		
	♀ old	♀	♂	♀ new	♀ old	♂	♀ new
1967 <i>Saxifraga oppositifolia</i>	49	1			2		
<i>Salix arctica</i> (♀ ♂)	20	1			1		
<i>Dryas integrifolia</i>	4	44	3		1	1	
<i>Cassiope tetragona</i>		10					
<i>Papaver radiculatum</i>		2	1				
<i>Pedicularis arctica</i>	30	9			5		
<i>Pedicularis capitata</i>	5	5			4		
<i>Melandrium affine</i>		1					
<i>Stellaria longipes</i>		1	6				1
<i>Silene acaulis</i>					1		
<i>Arnica alpina</i>		1					
<i>Polygonum viviparum</i>			1				
Total	108	75	11		14		2
1968 <i>Saxifraga oppositifolia</i>	23	3			4		
<i>Salix arctica</i> (♀ ♂)	36	1	2	1	1		
<i>Dryas integrifolia</i>	4	16			5		
<i>Cassiope tetragona</i>		13	3				
<i>Stellaria longipes</i>		10	7				
<i>Pedicularis arctica</i>	23	15			3		
<i>Pedicularis capitata</i>	19	19			2		
<i>Saxifraga tricuspidata</i>		8	2				
<i>Polygonum viviparum</i>			3				
<i>Arnica alpina</i>		1					
<i>Silene acaulis</i>					1		
<i>Epilobium latifolium</i>		8	18				
Total	105	94	35		16		

The main flowers at Lake Hazen which bumblebees visited for food are members of the species *Saxifraga oppositifolia*, *Cassiope tetragona*, *Pedicularis arctica*, *Pedicularis hirsuta*, *Salix arctica* (male and female), *Dryas integrifolia*, *Pedicularis capitata* and *Stellaria longipes*. Flowers of the species *Silene acaulis*, *Arnica alpina*, *Polygonum viviparum*, *Saxifraga tricuspidata* and *Epilobium latifolium* are occasionally visited near the end of a season when the more popular flowers are scarce. A few pollen grains of *Cerastium* sp. were collected late in the season from three honey pots of two nests, which indicates that these flowers were sparsely used for nectar. Flowers visited at the end of the season were those late in growing as indicated in the dates of flower phenology (Richards 1970). Thus the rapid active season affected flower phenology and flower visitation. At the end of the season, only nectar was collected from the flowers.

The composition of 70 pollen pellets was as follows: 35 consisted of pollen from one plant species; 27 of pollen from two plant species; 6 of pollen from three plant species and 2

of pollen from four plant species. I saw 459 bumblebees visit flowers during 1967 and 1968. Of these, 13 visited flowers of two species, and three visited flowers of three species. The rest yielded no evidence of having visited flowers of more than a single species. Foragers visited a wide range of flowers throughout the season, but at any one time they visited members of only a few species. For example, before workers emerged, queens visited only *S. oppositifolia* and *S. arctica* flowers, but when these flowers were scarce the foragers visited others.

In this study 254 samples of honey from 12 nests in 1967 were analyzed for sugar concentration. At Lake Hazen thick honey first appeared in nests when workers began to forage. The number of honey pots increased as the second and third brood larvae were being fed, but the numbers in use declined when the first males emerged. Most of the incoming nectar was placed in the honey pots from which the sexual adults fed. From queen acceptance of a nesting site until final brood decay, in one nest, the concentrations of total sugars tested, (Fig. 29) showed a gradual increase from thin to thick honey. Concentrations from other nests indicated this same trend. As expected, the mean honey concentrations varied from nest to nest and from honey pot to honey pot within the same nest on different days. Possible reasons for the difference in sugar concentration are water evaporation (Plath 1934) and quantitatively selective feeding (Free 1955b).

Total sugar concentrations of thin and thick honey are almost always higher, probably because of water evaporation, than are total sugar concentrations of nectar (Hocking 1953, 1968).

Adults of *B. polaris* and *B. hyperboreus* have been recorded to visit flowers of 43 species of plants distributed among 36 genera and 18 families. See Richards (1970, Appendix III) for a list of species names of plants visited.

Discussion.- The dependence of these bumblebees on flowers for nutrition is perhaps greater than the dependence of the flowers on bumblebees for pollination. Bees were recorded foraging for pollen and/or nectar from members of 15 plant species at Lake Hazen and from members of 36 genera in this and other arctic localities. This alone indicates that 'bees in the arctic tend to become less restricted in their choice of flowers' (Richards 1931) and that they 'specialize in being unspecialized' (Savile, pers. comm. 1969). The 50% constancy (35 out of 70) in flower visitation of these arctic bumblebees is in close agreement with the total figure given by Brian (1954) for various other members of *Bombus*, but is much higher than the figures given by Høeg (1924, 1929) although he analyzed the pollen from other parts of the body besides the corbiculae.

Almost all plants beyond the tree-line are self-fertile, and several are apomictic - necessary safeguards against frequent seasons when insect activity is severely restricted during the period of bloom (Savile, pers. comm. 1969). But, McAlpine (1965a) Hocking (1968) and Kevan (1970) have stated that a number of anthophilous Diptera are important arctic pollinators, a fact which indicates that some cross-pollination occurs in many flowering species. Hocking (1968) believes that flowers at Lake Hazen compete for pollination rather than that pollinators compete for nectar. Arctic bumblebees are pollinators only of those flowers from which they forage extensively. Other less important bumblebee-visited flowers are doubtful benefactors; however, there are exceptions such as *S. longipes* and *E. latifolium*.

As the presence and abundance of the arctic bumblebee-visited plant species vary within the Canadian Arctic archipelago and generally within the whole arctic, the usage by the bumblebees also varies. For example, *Silene acaulis* which several authors reported to be abundant and visited by bumblebees on Novaya Zemlya, was rare and rarely visited at Lake Hazen. Other examples are in the Cruciferae, Ericaceae, and especially Leguminosae. The

many possible ecological niches as yet unoccupied (McAlpine 1964, 1965a) are another reason for the variable usage by bumblebees.

NEST PARASITISM AMONG HIGH ARCTIC BUMBLEBEES

Bumblebees of the genus *Psithyrus* are known to parasitize nests of various species of *Bombus*, (Free and Butler, 1959) and intraspecific and interspecific nest parasitism has been recorded for *Bombus* (Hobbs, 1965a,b and 1967b). Yarrow (1970) suggests that *Bombus inexpectus* behaves like a workerless obligate parasite, similar to *Psithyrus*, but biological data are lacking. Reported here are observations establishing intra-specific nest parasitism in *B. polaris* and interspecific nest parasitism of *B. hyperboreus* on *B. polaris*. These findings are discussed in terms of the evidence they provide concerning origin and evolution of nest parasitism among bumblebees.

Intraspecific nest parasitism

In 13 natural nests a second *B. polaris* queen was found after the original queen had initiated and established a first brood. In each nest one of the two queens was dead. The nail polish markings on them established that in five instances the foundress was the victor of a previous fight; in three instances the intruder was victor; and in five, history of the victor was unknown. The intruding queens were observed nest-seeking as late as early emergence of first brood adults. These intruders did not initiate broods of their own but assisted the foraging workers. No disturbances, such as removal of larvae or destruction of egg cells, were noted in the nests. Milliron and Oliver (1966) reported one instance of intraspecific nest parasitism in *B. polaris*.

Nest parasitism by *Bombus hyperboreus*.

Interspecific associations of *B. polaris* and *B. hyperboreus* indicate a host-parasite relationship. Unlike other *Bombus* queens, those of *B. hyperboreus* do not establish nests of their own and do not produce workers over most of the range of the species. A solitary life with production of few or no workers was indicated for the sexual stages of *B. hyperboreus*, *B. balteatus* and *B. polaris* (Jacobson 1898; Friese, 1902, 1904, 1908, 1923a,b; Friese and Wagner, 1912). A parasitic mode of life was not suggested. Richards (1931) reported a worker to female ratio of 0.2, and Milliron and Oliver (1966) reported examining about a dozen museum specimens of *B. hyperboreus* workers, mostly from Scandinavian localities - probably the same material as was examined by Richards.

Other authors (Strand 1905; Richards 1931; Henriksen 1937, 1939; Brinck and Wingstrand 1951; Bruggeman 1958; Milliron and Oliver 1966 and I) reported only *B. hyperboreus* queens and males from various localities. Milliron and Oliver (1966) made preliminary observations at Lake Hazen on usurpation by *B. hyperboreus* females of nests of *B. polaris*. I made observations to determine if females of *B. hyperboreus* were parasitic on colonies of *B. polaris*.

Observations.- Individuals of *B. hyperboreus* emerged later in the season and were not as abundant as were individuals of *B. polaris*. Nest-seeking behavior was similar to that of *B. polaris*, except that *B. hyperboreus* queens did not initiate nests of their own.

Queen *B. hyperboreus* searched primarily along cracks in clay and in lemming holes for nesting sites of *B. polaris*, flying usually less than 25 cm above the ground. Most *B. hyperboreus* queens were seen previous to or after *B. polaris* workers of the first brood had emerged.

The following is a description of the behavior of a *B. hyperboreus* queen from the time of her first discovery of a *B. polaris* natural nest until she remained within the nest 58 minutes. The observation was made June 28, 1967, from 0030 to 0330 hours on a clear, calm, 9.0 C night in a marsh sedge meadow (M8, Fig. 6):

"The *B. hyperboreus* queen first approached the nest flying less than 25 cm high. She flew three or four orientation circles before landing and entering the 210° facing entrance. After defensive behavior (ie. rapid movement of the wings) by resident workers she retreated from the nest to a nearby moss clump where she groomed herself. Grooming consisted of rubbing the fore-and mid-legs over the head and thorax and hind-legs over the sides of the abdomen. She was repelled from the nest 13 times by the workers and queen before she gained acceptance. Twice the workers blocked the entrance to the intruding queen by lying upside down with the sting protruding and once two workers followed her about 60-75 cm from the nest. The *B. hyperboreus* queen, after being repelled from the nest, either groomed or visited flowers which were nearby. The grooming procedure was repeated many times. The *B. hyperboreus* queen did not orient back to the nest but flew directly."

I found in the nest at 0830 hours the same morning a *B. polaris* queen dead beside the honey pot and, near the nest entrance, eight *B. polaris* workers (either collecting pollen and nectar or warming the brood) eight first brood pupae near emergence and an active *B. hyperboreus* queen. During the examination the queen remained (except when I moved her) on top of a rough new egg cell built on the side of the incubation groove and containing seven horizontally laid eggs. As the queen appeared to be protecting this egg cell, I presumed she had laid the eggs. An arctic fox destroyed this nest two days later.

In five nests which had living *B. hyperboreus* queens, the host *B. polaris* queen was dead. More than one *B. hyperboreus* queen was collected in one nest with the latest nest-seeking queen alive. Seventeen dead *B. hyperboreus* queens were found in *B. polaris* nests as victims of an arctic fox. Milliron and Oliver (1966) reported two composite nests of *B. polaris* and *B. hyperboreus* sexuals, as adults or brood. They hypothesized that the establishing *B. polaris* queen was driven off by the usurping *B. hyperboreus* queen.

ADAPTATION OF BUMBLEBEES TO THE ARCTIC ENVIRONMENT

Characteristics of *Bombus polaris* may be regarded as a series of adaptations permitting members of this species to live under conditions imposed by the high arctic environment. Briefly stated, these conditions are: low temperature, small heat budget, reduced growing season with continuous or almost continuous daylight, and high water table with permafrost near the ground surface.

Normal nesting sites for bumblebees are abandoned nests of rodents, shrews or birds, either on or below the surface of the ground. In temperate areas, such sites provide warm shelter. In the high arctic, however, rodent nests (specifically those of lemmings) are unsuitable for bumblebees because they are cold and frequently wet. Although queens investigate these nests, they rarely use them, but instead nest in marsh and sedge meadows, which provide warm and dry sites, with an abundance of suitable nesting materials. The selection of these sites is an adaptation for life in the high arctic environment.

The relatively short period of growth available each year to arctic bumblebees is selective for rapid colony development. This could be achieved by increased rate of growth (ie., individual development), or by decreased time required to complete processes associated with development of the colony. Rate of development of individuals of *B. polaris* is the same as in more southern bumblebees, so the first alternative strategy was not adopted. Length of the annual life cycle was reduced by processes employing the second alternative. This re-

duction was achieved by production of only a single brood of workers prior to production of sexual forms; by a large first brood, providing proportionately more workers; by reduction in time required by the queen to provision first brood larvae and increase effectiveness of incubation; by laying all eggs in a single cell and feeding the larvae collectively; by a high rate of food provisioning, related to the more or less continuous foraging activities of workers in continuous daylight, and by acceptance of a wide variety of flowers by foragers. Structural and functional adaptations for flight at low temperature are the following: large size, long dense hair and dark coloration. These are factors which allow the bumblebees to be warmed by solar radiation. The relatively low height of flight of workers suggests that they attain additional warmth from the radiation reflected from the soil; at the same time they encounter lower wind speeds.

Members of *B. hyperboreus* exhibit structural and general behavioral features similar to those of *B. polaris*, so both species are similarly adapted for life in the arctic environment. Parasitic behavior patterns are special adaptations for life in an adaptive zone not restricted to one set of physical and biotic factors, and in this sense nest parasitism cannot be regarded as adaptive to the arctic. However, a parasitic mode of existence further shortens the annual life cycle of a species, and in this sense, it is adaptive in the far north. The intriguing question frequently asked: "Why are bumblebees found in the high arctic" can (perhaps) now be answered. Bumblebees and their host plants, being mutually dependant, must have dispersed northwards at the same time and during this process *B. polaris* and *B. hypoboreus* became adapted to environmental conditions that differed from those further south. These adaptations do not appear to involve large changes in physiology, morphology or behavior when the variation in the factors among all bumblebees is considered.

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REFERENCES

- Ander, von Kjell. 1965. Über die Verbreitung der Hummeln in Schweden (Hym. Apidae). Opusc. ent. 30: 135-139.
- Auclair, J. L., and C. A. Jamieson. 1948. A quantitative analysis of amino acids in pollen collected by bees. Science 108: 357-358.
- Betram, G. C. L. 1935. The low temperature limit of activity of arctic insects. J. Anim. Ecol. 4: 35-42.
- Braendegaard, J., K. L. Henriksen, and R. Spärck. 1935. Insects and Arachnids. Meddr Grønland 104 (16): 1-18.
- Brian, A. D. 1951. Brood development in *Bombus agrorum* (Hym., Bombidae). Entomologist's mon. Mag. 87: 207-212.

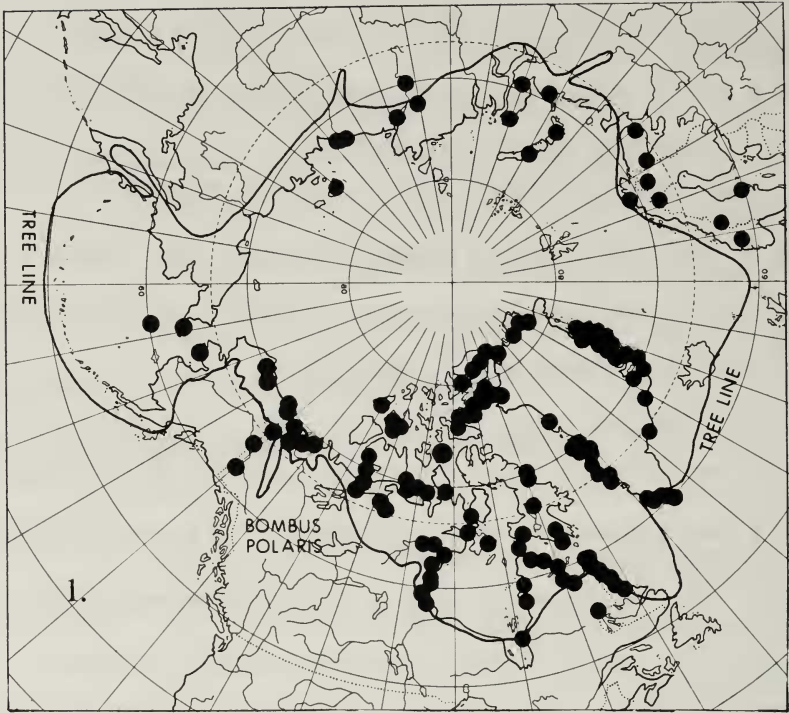
- Brian, A. D. 1952. Division of labour and foraging in *Bombus agrorum* Fabricius. *J. Anim. Ecol.* 21: 223-240.
- Brian, A. D. 1954. The foraging of bumblebees. *Bee Wld* 35: 61-67, 81-91.
- Brinck, P., and K. G. Wingstrand. 1949. The mountain fauna of the Virihaure area in Swedish Lapland. I General account. *K. fysiogr. Sällsk. Lund Förh* 60(2): 1-70.
- Brinck, P., and K. G. Wingstrand. 1951. The mountain fauna of the Virihaure area in Swedish Lapland. II Special account. *K. fysiogr. Sällsk. Lund Förh* 61(2): 1-173. Brinck, P. Hymenoptera Aculeata, p. 60-68.
- Bruggemann, P. F. 1958. Insects and environments of the high arctic. *Proc. X Int. Congr. Entomol.* (1956): 695-702.
- Bukatsch, F., and G. Wildner. 1956. Determination of ascorbic acid in nectar, pollen, parts of plants and elaisosomes, by a new micromethod. (in German). *Phyton* 7:37-46.
- Carpenter, G. D., and A. Holm. 1939. Insecta and Araneae collected in the Kangerdlugsuak Region of East Greenland by the British Expedition, 1935-36. *Ann. Mag. nat. Hist. ser.* 11, iii: 60-80.
- Chernov, Y. I. 1966. Complex of anthophilous insects in the tundra zone. (in Russian). In *problems of Geography, 69 organisms and natural environments.* p. 75-97.
- Church, N. S. 1960. Heat loss and the body temperature of flying insects. II. Heat conduction within the body and its losses by radiation and convection. *J. exp. Biol.* 37: 186-212.
- Clements, F. E., and F. L. Long. 1923. *Experimental pollination. An outline of the ecology of flowers and insects.* Pub. Carnegie Inst. Washington. No. 336. 274 p.
- Cockerell, T. D. A., and J. M'Nary. 1902. Notes on the mouth-parts of *Bombus*. *Can. Ent.* 34: 71-72.
- Corbet, P. S. 1966. Diel periodicities of weather factors near the ground in a high arctic locality: Hazen Camp, Ellesmere Island, N.W.T. Defence Research Board of Canada. *D. Phys. R. (G), Hazen* 29: 1-15.
- Corbet, P. S. 1967a. Screen temperatures during the summers 1962-1967 at Hazen Camp, Ellesmere Island, N.W.T. Defence Research Board of Canada. *D. Phys. R. (G), Hazen* 30: 1-11.
- Corbet, P. S. 1967b. Further observations on diel periodicities of weather factors near the ground at Hazen Camp, Ellesmere Island, N.W.T. Defence Research Board of Canada. *D. Phys. R. (G), Hazen* 31: 1-14.
- Cumber, R. A. 1949. The biology of humble-bees, with special reference to the production of the worker caste. *Trans. R. ent. Soc. Lond.* 100: 1-45.
- Cumber, R. A. 1953. Some aspects of the biology and ecology of humble-bees bearing upon the yields of red-clover seed in New Zealand. *N.Z. J. Sci. Technol.* 34: 227-240.
- Day, J. H. 1964. Characteristics of soils of the Hazen Camp area, Northern Ellesmere Island, N.W.T. Defence Research Board of Canada. *D. Phys. R. (G), Hazen* 24: 1-15.
- Digby, P. S. B. 1955. Factors affecting the temperature excess of insects in sunshine. *J. exp. Biol.* 32: 279-298.
- Downes, J. A. 1962. What is an arctic insect? *Can. Ent.* 94: 143-162.
- Downes, J. A. 1964. Arctic insects and their environment. *Can. Ent.* 96: 279-307.
- Downes, J. A. 1965. Adaptations of insects in the arctic. *A. Rev. Ent.* 10: 257-274.
- Ekstam, O. 1894. Zur Kenntnis der Blütenbestäubung auf Nowaja Semlja. *Öfvers. K. VetenskAkad. Förh.* 2: 79-84.
- Ekstam, O. 1897. Einige blütenbiologische Beobachtungen auf Nowaja Semlja. *Tromsø Mus. Arsh.* 18: 109-198.
- Ekstam, O. 1899. Einige blütenbiologische Beobachtungen auf Spitsbergen. *Tromsø Mus. Arsh.* 20: 1-66.

- Free, J. B. 1955a. The division of labour within bumblebee colonies. *Insectes soc.* 2: 195-212.
- Free, J. B. 1955b. The collection of food by bumblebees. *Insectes soc.* 2: 303-311.
- Free, J. B. and C. G. Butler. 1959. *Bumblebees*. Collins, London. 208p.
- Freuchen, P., and F. Salomonsen. 1958. *The arctic year*. Putnam, New York. 440 p.
- Friese, H. 1902. Die arktischen Hymenoptera mit Ausschluss der Tenthrediniden. In *Romer and Schaudin, Fauna arct. Jena* 2: 484-498.
- Friese, H. 1904. Über Hummelleben in arktischen Gebiete (Hym.). *Allg. Z. Ent.* 9: 409-414.
- Friese, H. 1908. Über die Bienen der Russischen Polar Expedition 1900-1903 und einiger anderen arktischen Ausbeuten. *Mem. Acad. Sci. St. Petersb. (Sci. Math. Phys. Nat.)* 18: 1-17.
- Friese, H. 1923a. Apidae p. 3-9. In scientific results of the Norwegian expedition to Novaya Zemlya 1921. (In German). *Nowaja Semlja Ekspedisjon No. 14*: 3-25.
- Friese, H. 1923b. Die europäischen Bienen (Apidae). *Das Leben und Wirken unserer Blumenwespen*. Walter de Gruyter and Co., Berlin and Leipzig. 456 p.
- Friese, H., and F. von Wagner. 1912. Zoologische Studien an Hummeln II. Die Hummeln der Arktik, des Hochgebirges und der Steppe. *Zool. Jb. Suppl.* 15: 155-210.
- Frison, T. H. 1919. Report of the Bremidae collected by Crocker Land Expedition, 1913-1917. *Bull. Am. Mus. nat. Hist.* 41: 451-459.
- Frison, T. H. 1927. A contribution to our knowledge of the relationships of the Bremidae of America north of Mexico (Hymenoptera). *Trans. Am. ent. Soc.* 53: 51-78.
- Fye, R. E., and J. T. Medler. 1954. Temperature studies in bumblebee domiciles. *J. econ. Ent.* 47: 847-852.
- Gary, N. E. 1967. A method of evaluating honey bee flight activity at the hive entrance. *J. econ. Ent.* 60: 102-105.
- Gavriliok, V. A. 1961. Duration of the period of fruiting and seed production in plants from S. E. Chukoth. (in Russian). *Bot. Zh.* 46: 90-97.
- Grant, V. 1950. The flower constancy of bees. *Bot. Rev.* 16: 379-398.
- Hasselrot, T. B. 1960. Studies on Swedish bumblebees (Genus *Bombus* Latr.) their domestication and biology. *Opusc. ent. Suppl.* 17 192 p.
- Hellén, W. 1933. Hymenoptera Aculeata aus Finnmarken in Norwegen. *Notul. ent.* 13: 41-43.
- Henriksen, K. L. 1937. Insects collected on the fifth Thule expedition. *Rept Fifth Thule Exp. 1921-1924. Copenhagen II* (8): 1-34.
- Henriksen, K. L. 1939. A revised index to the insects of Grønland. *Meddr Grønland* 119 (10): 1-119.
- Himmer, A. 1933. Die Nestwärme bei *Bombus agrorum* (Fabr.). *Biol. Zbl.* 53: 270-276.
- Hobbs, G. A. 1964a. Phylogeny of bumblebees based on brood-rearing behavior. *Can. Ent.* 96: 115-116.
- Hobbs, G. A. 1964b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. I Subgenus *Alpinobombus* Skor. *Can. Ent.* 96: 1465-1470.
- Hobbs, G. A. 1965a. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. II. Subgenus *Bombias* Robt. *Can. Ent.* 97: 120-128.
- Hobbs, G. A. 1965b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. III. Subgenus *Cullumanobombus* Vogt. *Can. Ent.* 97: 1297-1302.
- Hobbs, G. A. 1966a. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. IV. Subgenus *Fervidobombus* Skorifov. *Can. Ent.* 98: 33-39.
- Hobbs, G. A. 1966b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. V. Subgenus *Subterraneobombus* Vogt. *Can. Ent.* 98: 288-294.

- Hobbs, G. A. 1967a. Obtaining and protecting red-clover pollinating species of *Bombus* (Hymenoptera: Apidae). Can. Ent. 99: 943-951.
- Hobbs, G. A. 1967b. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VI. Subgenus *Pyrobombus*. Can. Ent. 99: 1271-1292.
- Hobbs, G. A. 1968. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VII. Subgenus *Bombus*. Can. Ent. 100: 156-164.
- Hobbs, G. A., W. O. Nummi, and J. F. Virostek. 1962. Managing colonies of bumblebees (Hymenoptera: Apidae) for pollination purposes. Can. Ent. 94: 1121-1132.
- Hocking, B. 1953. The intrinsic range and speed of flight of insects. Trans. R. ent. Soc. Lond. 104: 223-345.
- Hocking, B. 1968. Insect-flower associations in the high arctic with special reference to nectar. Oikos 19: 359-388.
- Hocking, B., and C. D. Sharplin. 1964. Bees at 82°N. Bee Wld 45: 144-146.
- Høeg, O. A. 1924. Pollen on humble-bees from Novaya Zemlya. Norsk. Novaya Semlia Exped. 1921 2(29): 1-18.
- Høeg, O. A. 1929. Pollen on humble-bees from Ellesmere Island. K. Norsk. Vidensk. Selsk. Forh. 11 (16): 55-57.
- Holmen, K. 1957. The vascular plants of Peary Land, North Greenland. Meddr Grønland 124(9): 1-149.
- Hügel, M. F. 1962. Étude de quelques constituants du pollen. Anns Abeille 5(2): 97-133.
- Jackson, C. I. 1959a. The meteorology at Lake Hazen Base Camp, Operation Hazen, narrative and preliminary reports 1957-1958. Defence Research Board of Canada. D. Phys. R. (G), Hazen 4: 1-88.
- Jackson, C. I. 1959b. The meteorology of Lake Hazen, N.W.T. Part I. Analysis of the observations. Defence Research Board of Canada, D. Phys. R. (G), Hazen 8: 1-194.
- Jackson, C. I. 1960. The meteorology of Lake Hazen, N.W.T. Part II. Synoptic influences, local forecasting, bibliography. Defence Research Board of Canada, D. Phys. R. (G), Hazen 9: 195-295.
- Jacobson, G. G. 1898. Zoological exploration on Novaya Zemlya in 1896. The insects of Novaya Zemlya. Mem. Acad. Sci. St. Petersburg. (Sci., Math., Phys.) 8: 171-244.
- Johansen, F. 1921. Report of the Canadian Arctic Expedition 1913-1918. Vol. III Insects Part K. Insect life on the western Arctic coast of America. 61 p. Kings Printers, Ottawa.
- Johansen, F., and I. C. Nielsen. 1910. The insects of the 'Danmark' expedition. Meddr Grønland 43(3): 35-68.
- Kevan, P. 1970. High arctic insect-flower relations. Ph.D. Thesis, University of Alberta.
- Knee, W. J., and J. T. Medler. 1965. Sugar concentration of bumblebee honey. Am. Bee J. 105(5): 174-175.
- Knuth, P. 1906-1909. Handbook of flower pollination. (Trans. by J. R. Ainsworth-Davis) 3 vol. Oxford, Clarendon.
- Løken, A. 1949. Bumblebees in relation to *Aconitum septentrionale* in central Norway (Oyer). Nytt Mag. Naturvid. 87: 1-60.
- Løken, A. 1954. Observations of bumblebee activity during the solar eclipse June 30, 1954. Univ. Bergen Pub. 13. Biol. Station. 6 p.
- Løken, A. 1961. Observations on Norwegian bumblebee nests (Hymenoptera, Apidae, *Bombus*). Norsk ent. Tidsskr. 11: 255-268.
- Longstaff, T. G. 1932. An ecological reconnaissance in West Greenland. J. Anim. Ecol. 1: 119-142.
- Lubliner-Mianowska, K. 1956. Investigations on the chemical composition of pollen. I. The study of pollen as bee food. Acta Soc. Bot. Pol. 25: 409-419. From Apic. Abstr. 376/57.

- Marling, A. 1956. The effect of honey guides. *Behavior* 9: 114-139.
- Marler, P. R., and W. I. Hamilton. 1967. *Mechanisms of animal behavior*. J. Wiley and Sons, Inc. New York. 771 p.
- McAlpine, J. F. 1964. Arthropods of the bleakest barren lands: composition and distribution of the arthropod fauna of the Northwestern Queen Elizabeth Islands. *Can. Ent.* 96: 127-129.
- McAlpine, J. F. 1965a. Insects and related terrestrial invertebrates of the Ellef Ringnes Island. *Arctic* 18: 73-103.
- McAlpine, J. F. 1965b. Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. *Can. Fld Nat.* 79: 247-252.
- McLachlan, R. 1879. Report on the insecta (including Arachnida) collected by Captain Feiden and Mr. Hart between the parallels of 78 and 83 north latitude, during the recent arctic expedition. *J. Linn. Soc. (Zool.)* 14: 98-122.
- Medler, J. T. 1962a. Development and absorption of eggs in bumblebees (Hymenoptera: Apidae). *Can. Ent.* 94: 825-833.
- Medler, J. T. 1962b. Morphological analysis of bumblebee mouthparts. *Trans. XI Int. Cong. Ent.* 1960: 517-521.
- Medler, J. T. 1965. Variation in size in the worker caste of *Bombus fervidus* (Fab.). *Proc. XII Int. Congr. Ent.* 1964: 388-389.
- Michener, C. D., and W. E. LaBerge. 1954. A large *Bombus* nest from Mexico. *Psyche* 61: 63-67.
- Milliron, H. E., and D. R. Oliver. 1966. Bumblebees from Northern Ellesmere Island, with observations on usurpation by *Megabombus hyperboreus* (Schönh)(Hymenoptera: Apidae). *Can. Ent.* 98: 207-213.
- Mosquin, T., and J. E. H. Martin. 1967. Observations on the pollination biology of plants on Melville Island, N.W.T. Canada. *Can. Fld Nat.* 81: 205-210.
- Newport, G. 1837. On the temperature of insects, and its connection with the functions of respiration and circulation in this class of invertebrate animals. *Phil. Trans. R. Soc.* 1837: 259-338.
- Nielsen, E. T. 1938. Temperature in a nest of *Bombus hypnorum* L. *Vidensk. Meddr Dansk naturh. Foren.* 102: 1-6.
- Oliver, D. R., and P. S. Corbet. 1966. Aquatic habitats in a high arctic locality: the Hazen Camp study area, Ellesmere Island N.W.T. Defence Research Board of Canada. *D. Phys. R. (G)*, Hazen 26: 1-115.
- Park, O. W. 1930. Variations in the concentrations of floral nectars. *J. econ. Ent.* 23: 440-441.
- Plath, O. E. 1934. *Bumblebees and their ways*. MacMillan, New York. 201 p.
- Porsild, A. E. 1964. Illustrated flora of the Canadian Arctic Archipelago. *Bull. natn. Mus. Can.* 146: 1-218.
- Powell, J. M. 1961. The vegetation and microclimate of the Lake Hazen area, Northern Ellesmere Island N.W.T. Defence Research Board of Canada. *D. Phys. R. (G)*, Hazen 14: 1-122.
- Richards, K. W. 1970. *Biological Studies of Arctic bumblebees*. M.Sc. thesis, University of Alberta, Edmonton, Canada. 165 p.
- Richards, O. W. 1931. Some notes on the humble-bees allied to *Bombus alpinus* L. *Tromsø Mus. Arsh.* 50 (6): 1-32.
- Richards, O. W. 1968. The subgeneric divisions of the genus *Bombus* Latreille (Hymenoptera: Apidae). *Bull. Br. Mus. nat. Hist. (Ent.)* 22: 209-276.

- Savile, D. B. O. 1959. The botany of Somerset Island, District of Franklin. *Can. J. Bot.* 37: 959-1002.
- Savile, D. B. O. 1964. General ecology and vascular plants of the Hazen Camp area. *Arctic* 17: 237-258.
- Schwartz, I., and A. Kock. 1954. Comparative analysis of the most important growth vitamins in flower pollen. (in German). *Wiss. Z. Univ. Halle, Math-Nat.* 4:7-20. *From Apic. Abstr.* 306/60.
- Shuel, R. W. 1967. The influence of external factors on nectar production. *Am. Bee J.* 107 (2): 54-56.
- Skorikov, A. S. 1937. Die grönländischen Hummeln im Aspekte der Zirkumpolarfauna. *Ent. Meddr* 20: 37-64.
- Sladen, F. W. L. 1912. The humble-bee its life history and how to domesticate it. MacMillan, London, 283 p.
- Sladen, F. W. L. 1919. The wasps and bees collected by the Canadian Arctic Expedition, 1913-1918, vol. III Insecta, Part G. Hymenoptera and Plant Galls: 25-35. Kings Printers Ottawa.
- Sørensen, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. *Meddr Grønland* 125: 1-305.
- Sørensen, T. 1954. Adaptations of small plants to deficient nutrition and a short growing season. *Bot. Tidsskr.* 51: 339-361.
- Sparre-Schneider, J. 1906. Hymenoptera aculeata im arktischen Norwenge. *Tromsø Mus. Arsh.* 29: 81-160.
- Strand, E. 1905. Coleoptera, Hymenoptera, Lepidoptera und Araneae. Kristiania, Report of the Second Norwegian Arctic Expedition in the Fram 1898-1902. 3: 1-30.
- Swales, D. E. 1966. Species of insects and mites collected at Frobisher Bay, Baffin Island 1964 and Inuvik, N.W.T., 1965 with brief ecological and geographical notes. *Ann. ent. Soc. Queb.* 11: 189-199.
- Thawley, A. R. 1969. The components of honey and their effects on its properties: a review. *Bee Wld* 50: 51-60.
- Weaver, N., and K. A. Kuiken. 1951. Quantitative analysis of the essential amino acids of royal jelly and some pollens. *J. econ. Ent.* 44: 635-638.
- Wojtowski, F. 1963a. Observations on the biology and reproduction of bumblebees (Bombinae). *Zoologica Pol.* 13: (½): 3-18.
- Wojtowski, F. 1963b. Studies on heat and water economy in bumblebees' nests (Bombinae). *Zoologica Pol.* 13(½): 19-36.
- Wykes, G. R. 1950. Nectar secretion researches. *Australas. Beekpr* 52: 67-68.
- Wykes, G. R. 1951. Some aspects of nectar secretion. *Int. Beekpr Congr.* 14: 1-4.
- Wykes, G. R. 1952a. An investigation of the sugars present in the nectar of flowers of various species. *New Phytol.* 51: 210-215.
- Wykes, G. R. 1952b. The influence of variation in the supply of carbohydrate on the process of nectar secretion. *New Phytol.* 51: 294-300.
- Wykes, G. R. 1952c. The preferences of honeybees for solutions of various sugars which occur in nectar. *J. exp. Biol.* 29: 511-519.
- Yarrow, I. H. H. 1955. *Bombus (Alpinobombus) hyperboreus clydensis* n. ssp. from Baffinland, Northwest Territories, Canada. *Ann. Mag. nat. Hist.* 12(8): 151-152.
- Yarrow, I. H. H. 1970. Is *Bombus inexpectus* (Tkalcu) a workless obligate parasite? (Hym. Apidae). *Insects soci.* XVII (2): 95-112.



Figs. 1-2. Geographical distribution maps. 1. *Bombus (Alpinobombus) polaris* Curtis. 2. *Bombus (Alpinobombus) hyperboreus* Schönherr.

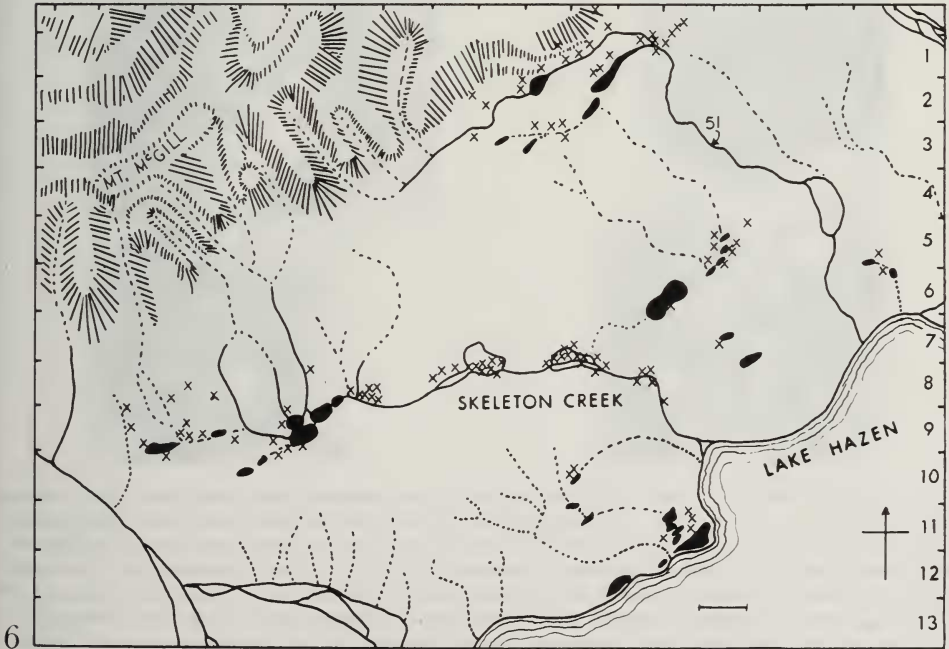
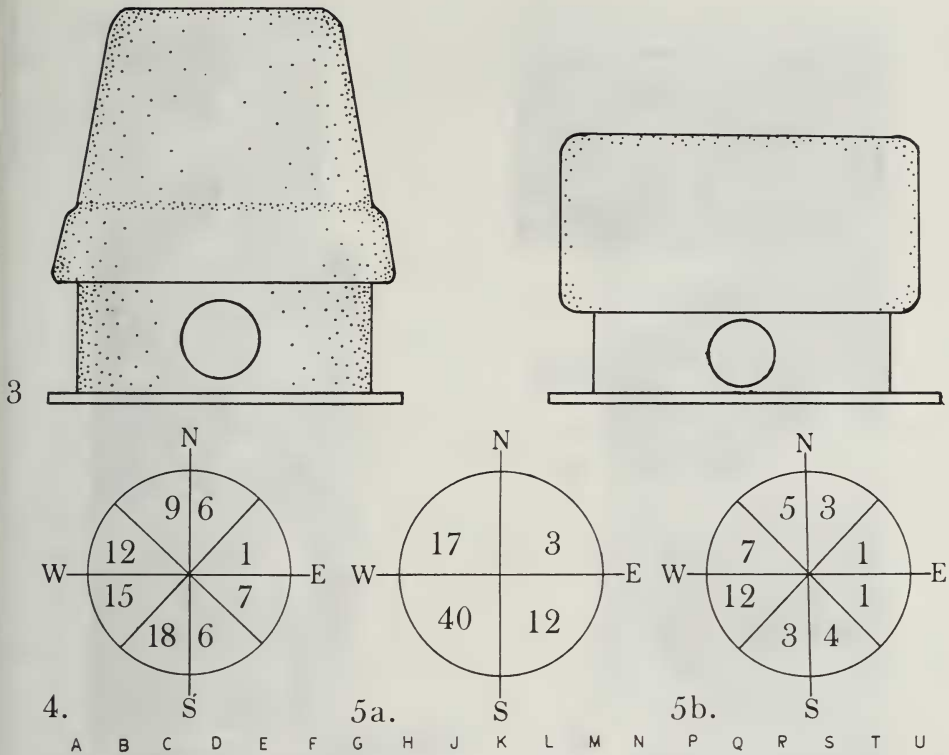


Fig. 3. Two basic types of small, light weight artificial domiciles, one-half size. Fig. 4. Numbers of *B. polaris* queens investigating different lemming holes by points of the compass at Lake Hazen, N.W.T., 1967 and 1968. Fig. 5. Generalized hummock or moss mound, numbers of nests of *B. polaris*: a, by quarter hummock or moss mound; b, number of nest exits by compass point. Fig. 6. Distribution of *B. polaris* natural nests (marked X) in the Lake Hazen study area. Map modified from Savile (1964). Accompanying scale divisions equal 1000 feet.

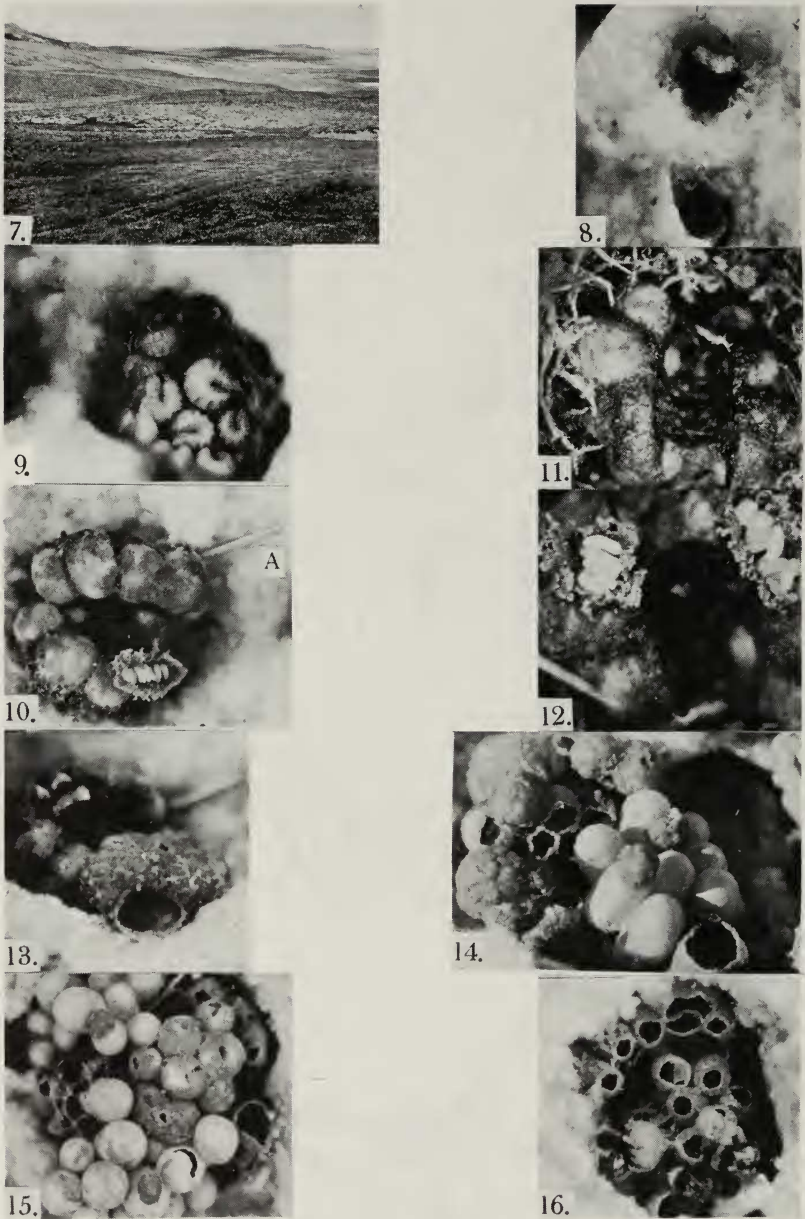
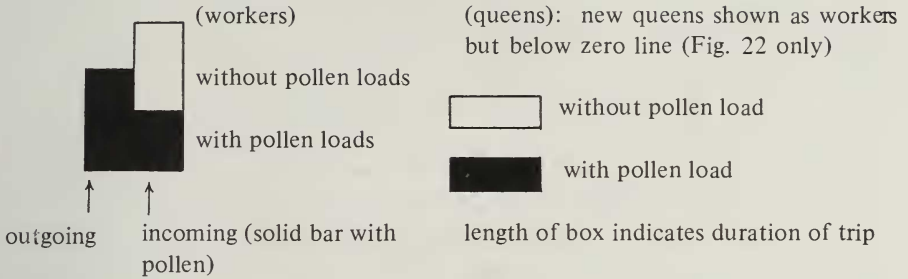


Fig. 7. Typical marsh and sedge meadow (K8) in which *B. polaris* queens established natural nests. Stakes indicate location of nests. Fig. 8. First brood cell of *B. polaris* with honey pot and brood with wax-pollen canopy intact. Fig. 9. Exposed first brood larvae showing curled position. Fig. 10. Second brood (male) eggs on top of first brood cocoons; the eggs have been exposed to show their horizontal orientation. A—thermistor probe. Fig. 11. Second brood egg cells on the outside tops of the cocoons that formed the sides of the incubation groove. Fig. 12. Same brood cells as Fig. 11. with the two groups of eggs exposed showing the front half of the incubation groove covered first. Fig. 13. Close-up of pollen receptacle on the side and beneath the second brood (male) larvae. Fig. 14. Egg cells of the third brood (queen) on top of the newly spun male cocoons. The large pollen receptacle is beside and beneath the male cocoons. Fig. 15. Brood exposed showing male cocoons (center top and bottom), exposed last-instar queen larvae (right), egg cells on top of male cocoons, and pollen receptacle (extreme right). Fig. 16. All but one queen egg cell (left) emerged, and many honey pots (top center) nearly empty. A varying time lag is apparent in nest temperature changes resulting from external events. This is attributable to varying low conductivity of nest material plus thermometer response time.

Figs. 17-26. Flight activity, weather, and nest temperature of *B. polaris*, 1968, at Lake Hazen, N.W.T.

Explanation of symbols:

Flight activity:



Temperature, air \times — \times , in artificial domicile nest \bullet — \bullet — \bullet ,

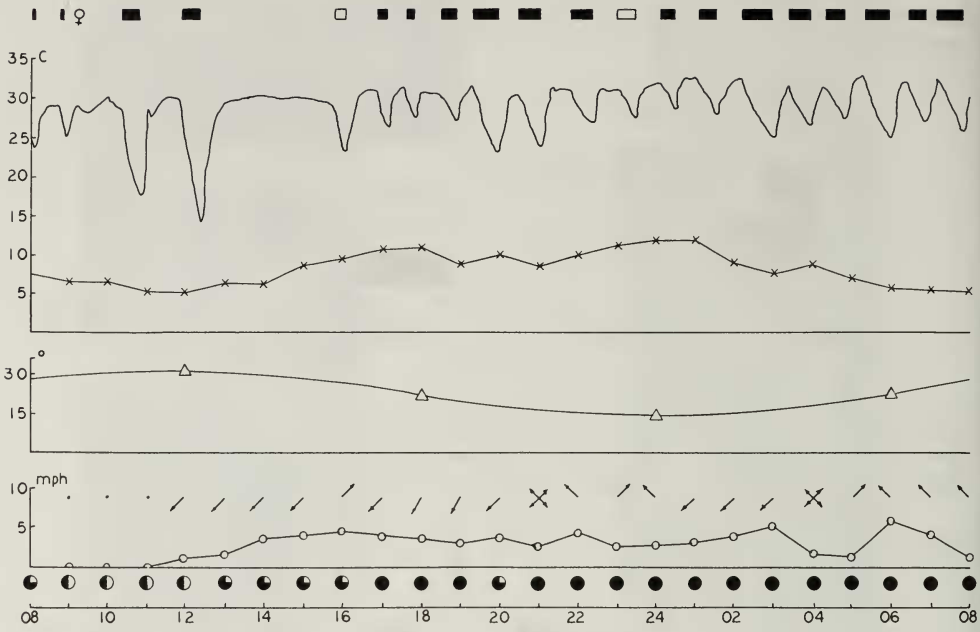
Temperature in nest; continuous —, 30 minute mean \bullet — \bullet

Angular elevation of sun from Corbet (1966): Δ

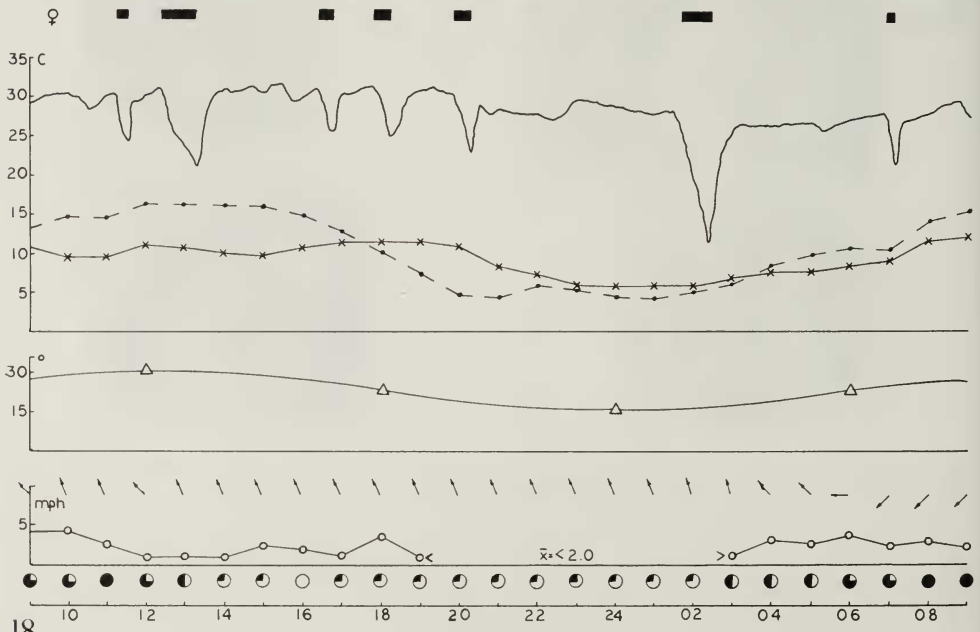
Wind direction \uparrow , \leftarrow E, \downarrow , \rightarrow W, variable \times , velocity in mph \circ ,
 S
 N

Cloud cover 0/8 \bigcirc , 2/8 $\frac{1}{4}$ \bigcirc , 4/8 $\frac{1}{2}$ \bigcirc , 6/8 $\frac{3}{4}$ \bigcirc , 8/8 \bullet , rain \bullet (Fig. 22 only)

Time: eastern standard, 00=24=midnight.



17.



18.

Fig. 17. June 23-24, 1968; one queen; 17 first brood larvae. Fig. 18. June 30-July 1, 1968; one queen, 17 first brood pupae, 10 second brood eggs. For explanation of symbols see page 149

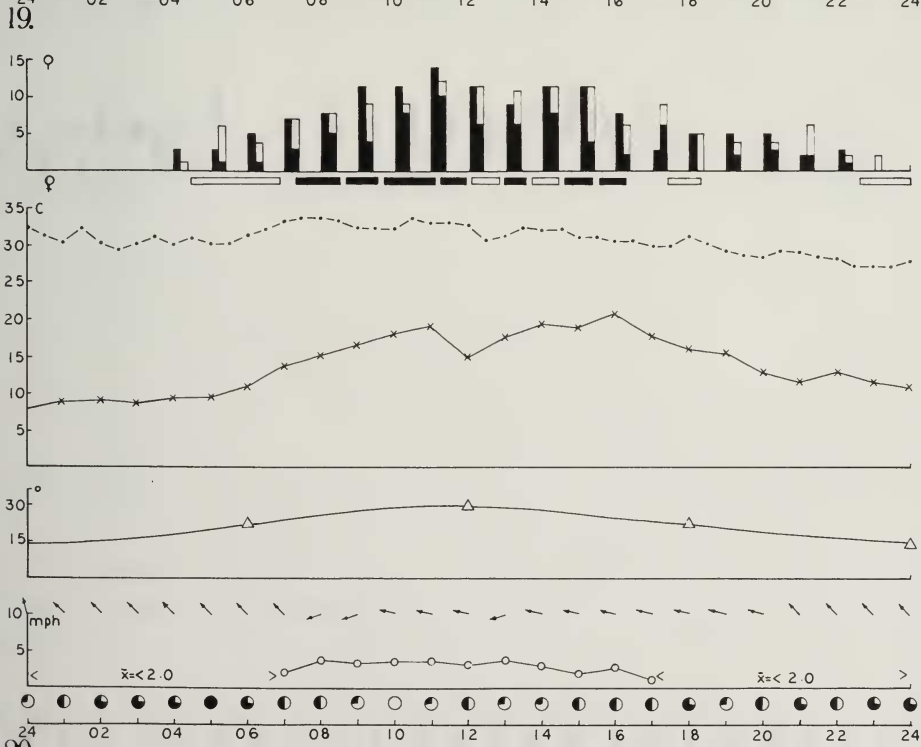
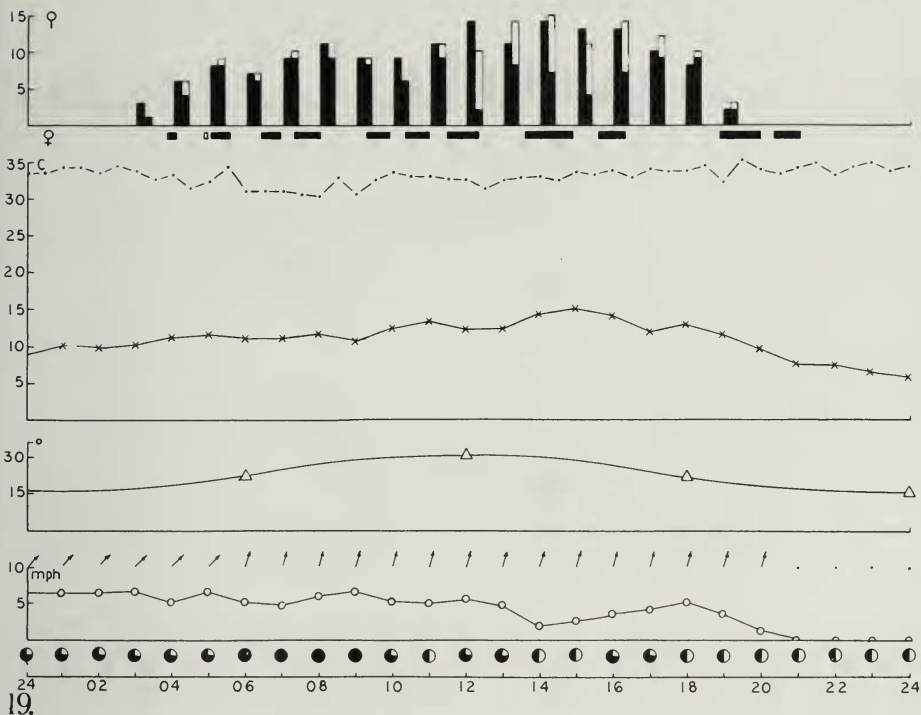


Fig. 19. July 6, 1968; one queen, 16 workers, second brood of 14 late-instar larvae, 10 early pupae, third brood of 10 eggs.
 Fig. 20. July 12, 1968; one queen, 14 workers, second brood of 24 late-pupae, third brood 6 eggs, 10 mid-larvae. For explanation of symbols see page 149

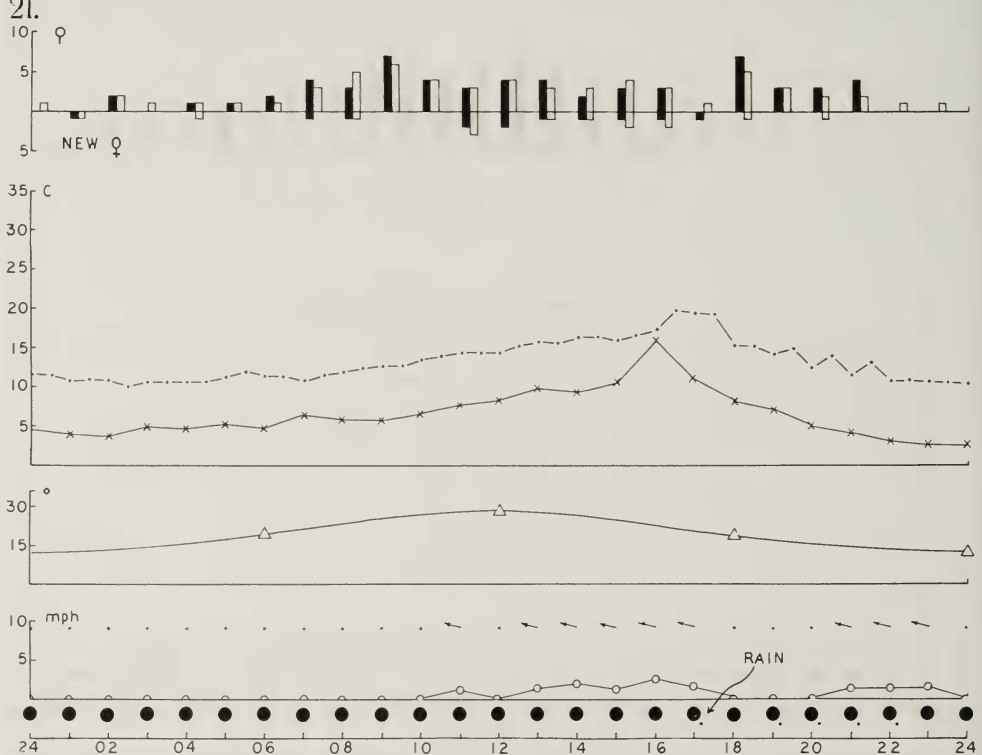
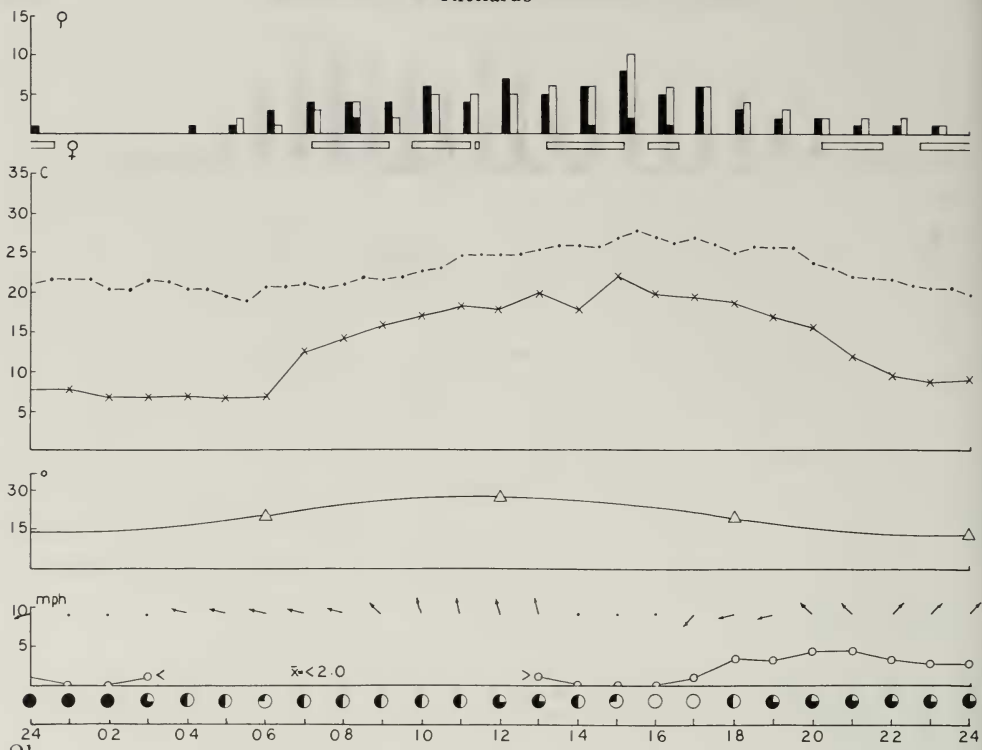
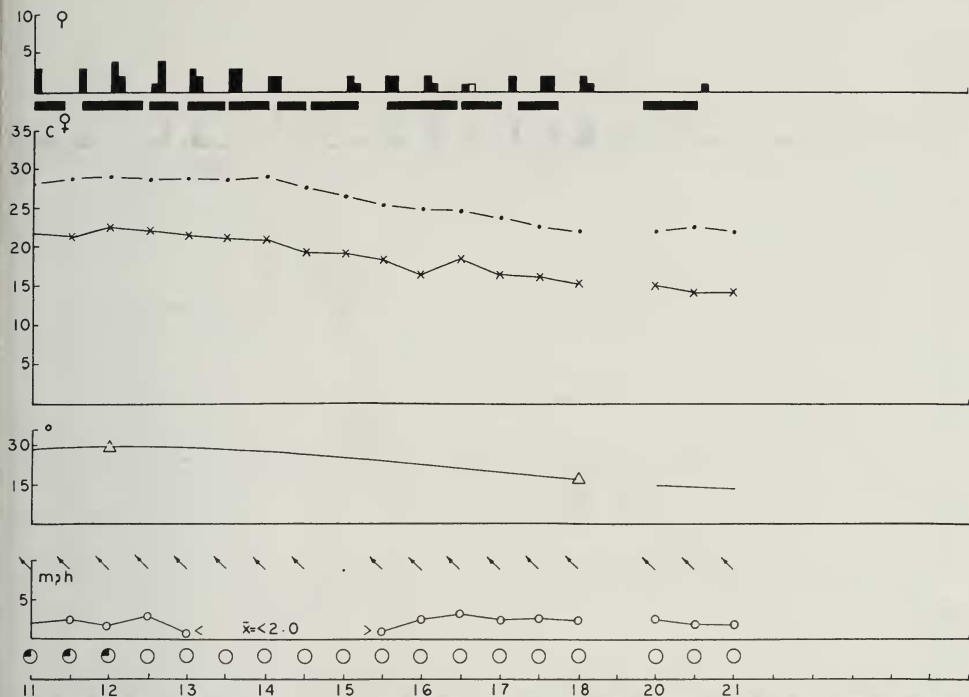
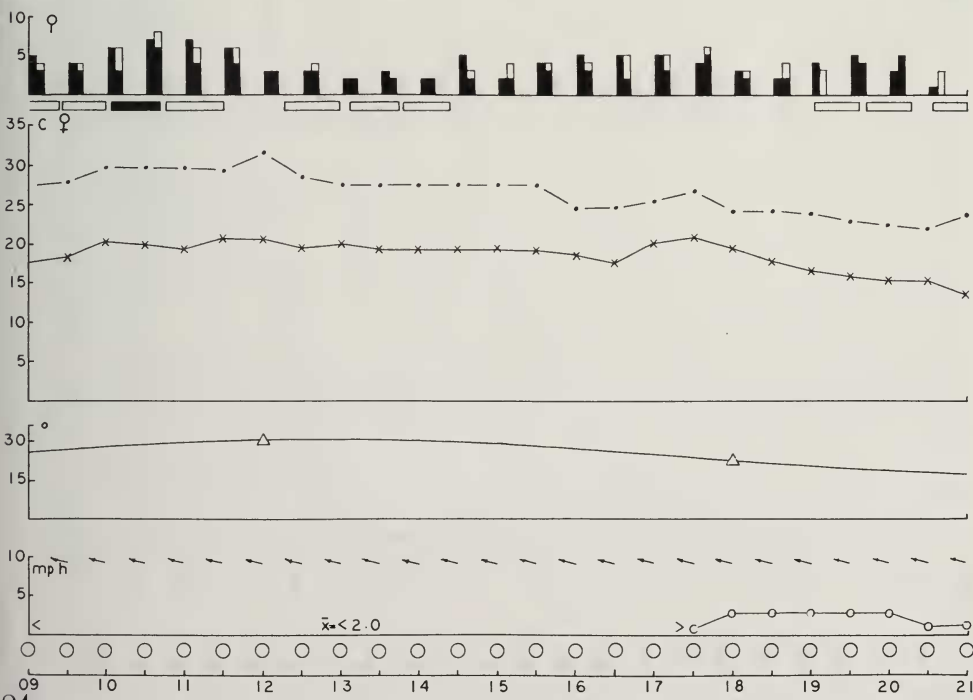


Fig. 21. July 18, 1968; one queen, 10 workers, 3 males, second brood 21 late-pupa, third brood 6 eggs, 10 pupae. Fig. 22. July 24, 1968; 9 workers, 5 fall queens, 2 males, third brood 5 late-pupa. For explanation of symbols see page 149



23.



24.

Fig. 23. July 9, 1968; one queen, 14 workers. Fig. 24. July 11, 1968, one queen, 14 workers. For explanation of symbols see page 149

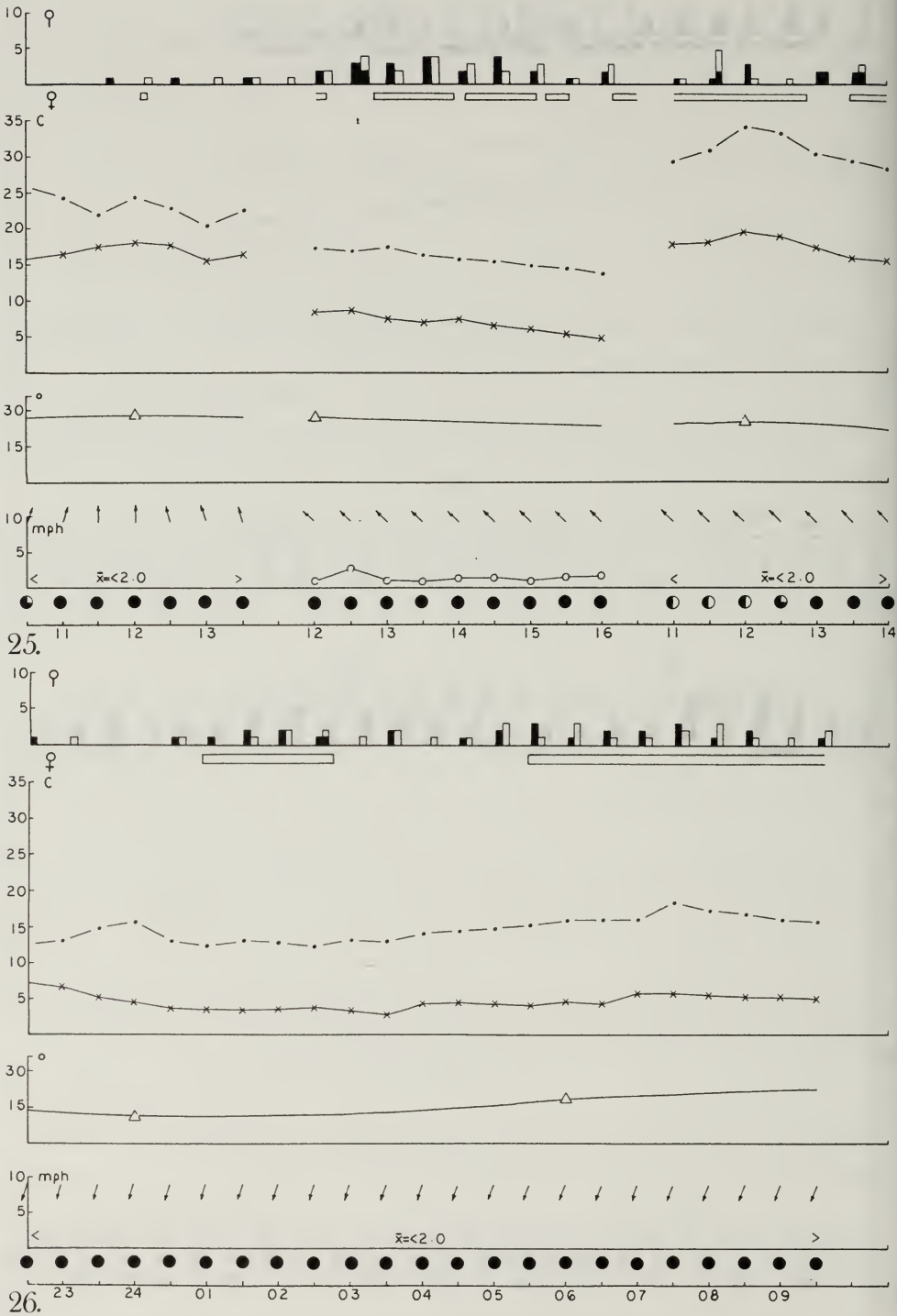


Fig. 25. July 14, 15, 1968; one queen, 10 workers. Fig. 26. July 21, 1968; one queen, 8 workers. For explanation of symbols see page 149

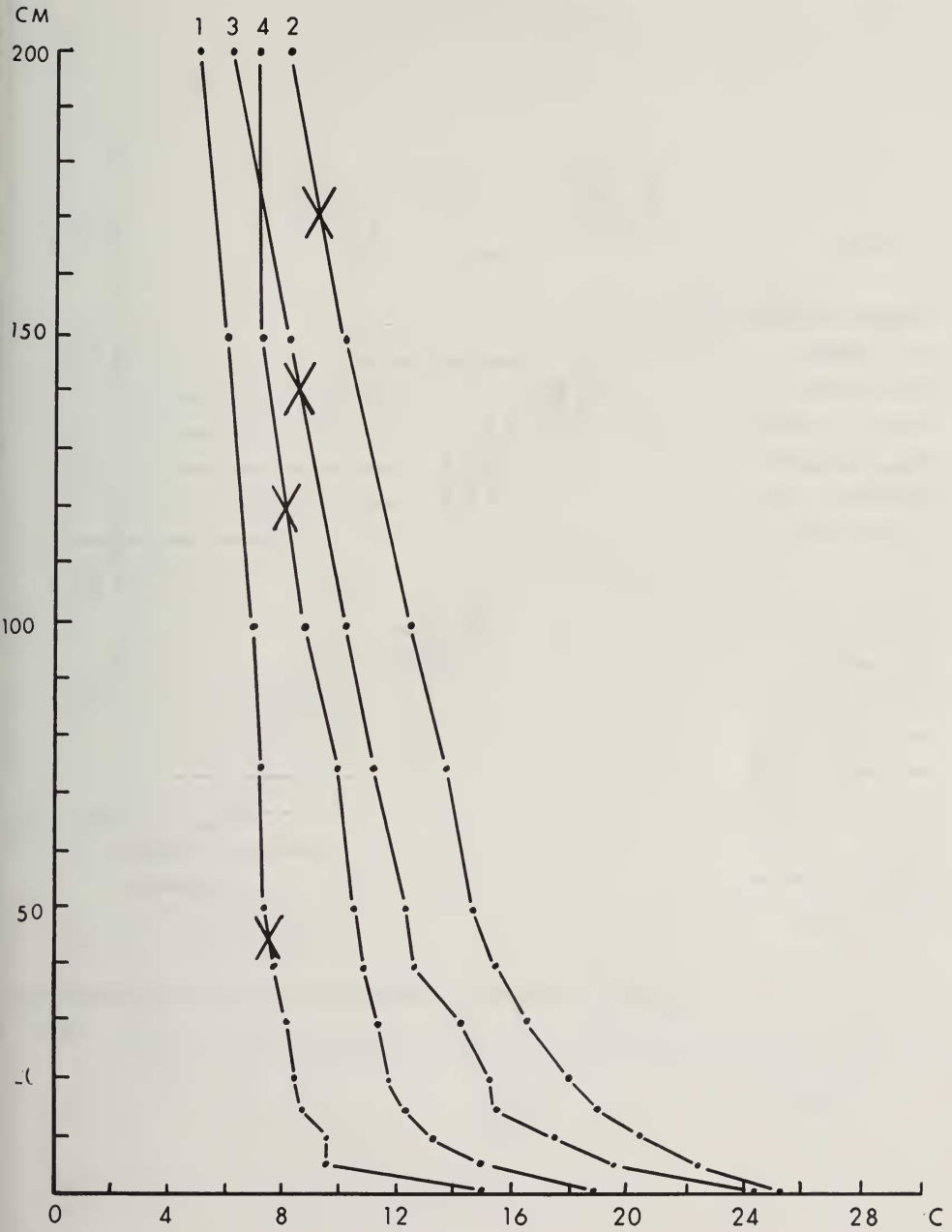


Fig. 27. Profile of air temperatures on 1. June 30, 2. July 5, 3. July 15, and 4. July 31, 1968. X—estimated mean height of flight of queens and workers.

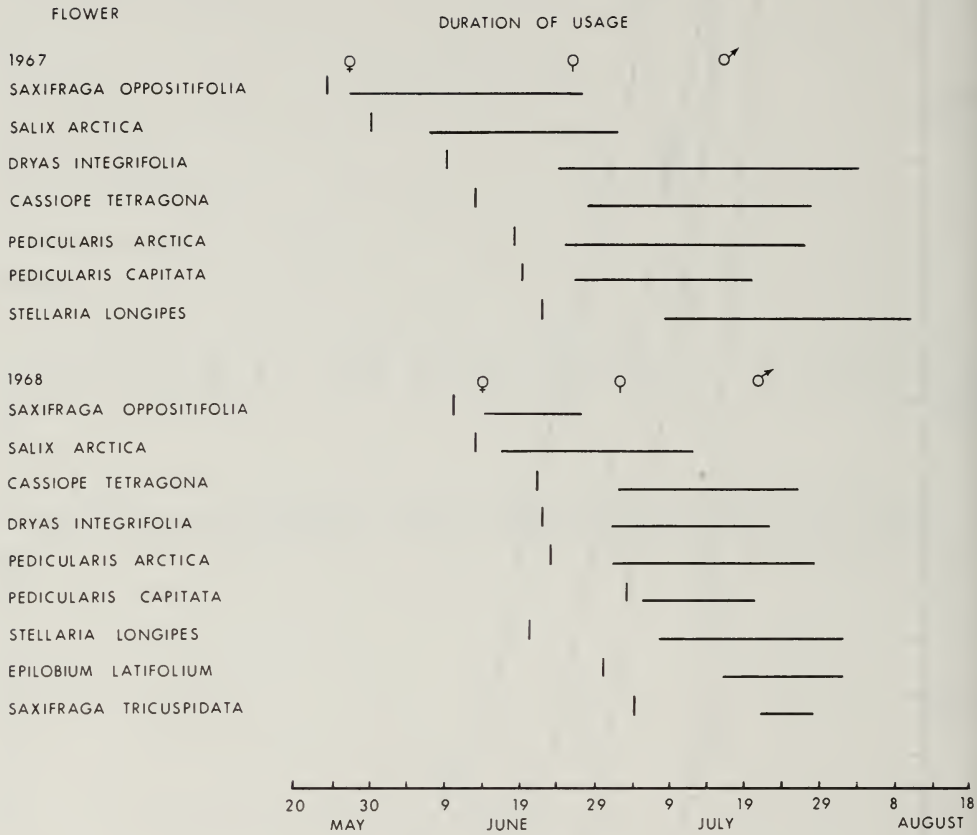


Fig. 28. Period of utilization for 1967 and 1968 of the major bumblebee flowers at Lake Hazen. Vertical lines and symbols indicate first appearance of flowers and caste or sex of bees respectively.

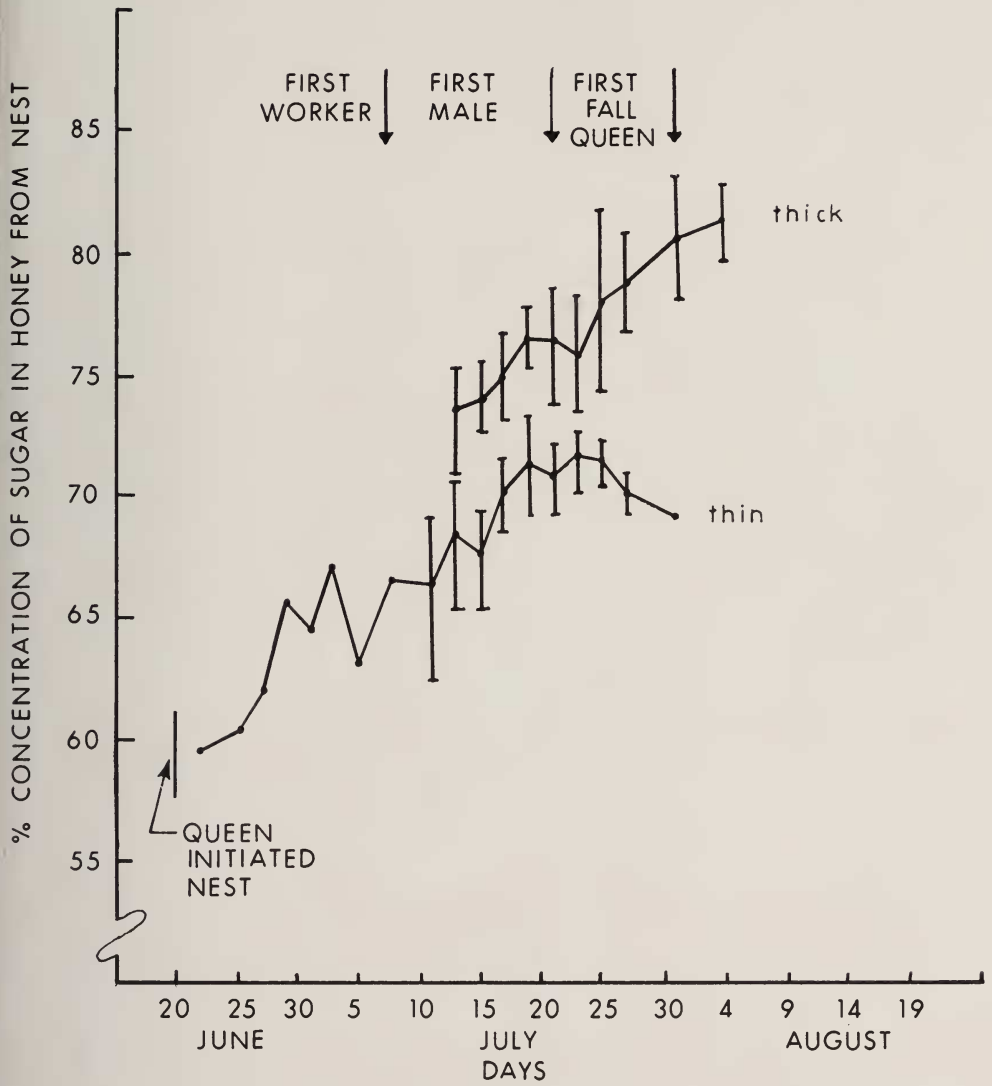


Fig. 29. The concentration of sugars from thin and thick honey from one nest. Vertical lines indicate one SD each side of mean. Arrows indicate first appearance of bees in nest.

